The Effects Of Grazing on the Recovery of Plant-Pollinator Systems Following Fire in the Mediterranean

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Abstract

This study was carried out in phrygana and maquis habitats of the Eastern Mediterranean (hot-spots for bee diversity), to assess grazing impacts on bee communities in habitats also experiencing frequent wildfires, and to explain the mechanisms of such effects.

On Mount Carmel, Israel, in 1999 and 2000, habitats with varying intensities of cattle grazing and post-burn age were surveyed. Bee diversity and abundance were measured, together with grazing levels, floral diversity and abundance, nectar and pollen rewards and vegetation structure. On the Island of Lesvos, in 2001, the effects of grazing on vegetation structure and reward production of two shrub species were investigated. Exclosures were used in both sites to show the immediate effects on flowers of removing livestock form formerly grazed areas.

Close relationships were found between bee diversity and abundance and flower diversity and abundance, bee abundance being better explained by the previous year's flower abundance. Bee abundance also increased with pollen abundance, but not with nectar availability. Bee and flower species richness were highest at moderate grazing intensities, but abundance, increased even at the highest intensities. Path-analysis showed that the effects of both grazing and fire on bee diversity occurred mainly via changes in herb flower diversity. Conversely, bee abundance was affected mainly by changes in halictid bees, which became more numerous in grazed sites, where ground was compacted and composites were abundant.

Grazing also created a mosaic of tall scrub and open patches of herbs. This "patchiness" helped maintain a diverse herb flora. Studies of *Cistus creticus* and *Lavandula stoechas* in Lesvos showed that shrub species also produced more flowers, and higher rewards, at patch edges.

Overall, bee communities benefit from a relatively high level of grazing in phrygana, and may be further increased if grazing pressure is relaxed during the peak flowering season.

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Contents

1 General Introduction

1.1 Disturbance by Fire and Grazing.

The role of natural disturbance has been well documented in many types of vegetation (Reviewed by White 1979; Sousa 1984; Pickett & White 1985; Freedman 1989; Huston 1994). In many parts of the world, disturbance by both fires and grazing are important in maintaining a balance between different species and therefore in maintaining diversity. However, due to the activities of man, the scale and frequency of these types of disturbance have changed so that in some cases this natural balance may have been upset (Grubb *et al.* 1986; Naveh 1990). Both fire and grazing may be regarded as agents of widespread disturbance, since both reduce the amount of biomass over large areas (Noy-Meir 1995); however, several studies suggest that fire and grazing have distinct but interactive effects on diversity (Collins & Barbour 1985; Collins 1987; Noy-Meir 1995).

Overgrazing is linked with soil erosion on arid lands the world over (Grubb 1986) and can lead to irreversible changes in vegetation or desertification (Newman 1993). Since it is widespread year after year, overgrazing can be a greater problem than is fire (Ellison 1960; Belsky 1992) which occurs more sporadically. The influence of grazing on vegetation may be exerted by trampling, fertilizing the soil by dung an urine or introducing plants from elsewhere by carrying seeds on coats or hooves, but most obviously it operates by defoliation. Generally speaking, grazers are selective about what they eat and the effect of grazing certain (most palatable) plant species in a community is to handicap those species and encourage others so that the composition of species is changed (Ellison 1960; Krebs 2001; McNaughton 1984; Newman 1993).

Fire, on the other hand is less selective and although it opens up the vegetation, which allows adventitious species to colonize, in Mediterranean habitats these are usually rapidly eliminated after the regeneration of the species which were present before the fire (Trabaud *et al.* 1980; Schiller *et al.* 1997). Fire therefore tends to "reset" the vegetation so that as long as all species still exist, in the seed bank or as roots, the vegetation can return to its composition before burning. Fire in Mediterranean habitats can consequently be a rather superficial phenomenon as far as floristic composition is concerned, although the number of annuals and the species richness may temporarily increase during the first few post-burn years (Trabaud *et al.* 1980; Schiller *et al.* 1997).

Some habitats have experienced frequent grazing and burning events for thousands of years; therefore many species have attributes that enable them to tolerate or take advantage of these disturbances (Naveh 1974; Fuentes & Etchegaray 1983). Adaptations that enhance survival at high grazing levels may be similar to those which help plants to tolerate arid environments. For example in grasses, having basal meristems, small stature, below-ground nutrient reserves and rapid growth may allow them to tolerate grazing as well as drought (Coughenor 1985). These and other adaptations to herbivory such as prostrate shoots and rosette forms, with renewal buds close to or below ground, short growing seasons and annual or short-perennial life cycles allow plants to survive in spite of grazing (Smith & Smith 2001). Chemical defences (usually secondary metabolic products which are toxic to herbivores) and/or morphological defences such as spines, mean that some plants are unpalatable and less likely to be eaten (Noy-Meir 1989; Smith & Smith 2001). However, palatability may vary depending on the species of grazer and the time of year (e.g. Harrington,

1982). For example, whether a species is grazed also depends on its relative palatability compared to what other forage is available (MacDonald *et al.*1998). Plants with the characteristics described above are hereafter referred to as 'grazing-adapted'.

Many plants also have adaptations that allow them to tolerate fire and in some species seed dispersal or germination only occur in response to fire. For example, many conifers have serotinous cones, which only open at the high temperatures caused by fire (Aber & Melillo 2001). Other woody species such as *Eucalyptus* increase habitat flammability and have seeds which germinate rapidly in response to fire, therefore gaining a competitive advantage over other species. For Mediterranean conifers like *Pinus halipensis* and *P. brutia* fire provides the only opportunity for regeneration under a dense maquis understorey (Naveh 1990). Other species are "post-fire re-sprouters" and have viable belowground buds which enable them to root sprout following fire (Aber & Melillo 2001; Naveh 1990).

1.1.1 Fire and Grazing in Mediterranean Habitats.

In Mediterranean habitats, intensive grazing, fire cycles and cutting have drastically changed the natural vegetation (Naveh 1982; Trabaud 1982; Cody 1986) and created a mosaic of ecosystems representing different stages of degradation and succession (Di Castri 1981). These range from rich, multi-layered semi-open woodlands, shrublands and grasslands, to depleted, one-layered phrygana (scrub) and maquis (woodland) or man-made rock deserts (Naveh 1982).

When kept at a moderate level as in past times, grazing may contribute to ecosystem function (Petanidou & Ellis 1996), helping to maintain an equilibrium between the different woody and herbaceous strata (Naveh 1982) but in extreme cases, overgrazing can lead to soil erosion and desertification (Petanidou and Ellis 1996). In Mediterranean countries now about 90% of sheep and goat food requirements are met by free grazing (Pulina *et al.* 1995) and their grazing is almost uncontrolled, seriously affecting the environment (Giourga *et al.* 1998). In some areas such as Crete, hundreds of years of intensive grazing have resulted in severe land degradation (Hill 1998) and Petanidou and Ellis (1996) believe overgrazing to be one of the most serious threats to the Mediterranean landscape as a whole.

Fire is also a major disturbance, though it is necessary at some level to initiate secondary succession or regeneration, to maintain plant and animal diversity and to ensure the survival of fire-dependent organisms (Esseen *et al.* 1992). In recent years, however, there has been prolonged protection of Mediterranean shrublands, aimed at re-creating what was believed to be the natural "maquis forest climax" (Naveh 1982). However complete protection from fire has led to impoverished plant communities (Bond 1980) and the expansion of these maquis pine forests which are highly flammable (Naveh 1982; Schiller *et al.* 1997). The extent of these forests, along with tourism and mass recreation, have depleted diversity and aggravated fire hazards, so that in some areas fires are becoming larger and more frequent than ever (Naveh 1982). Fire frequency is crucial for many plants; for example on Arnhem plateau (monsoonal northern Australia) Russel-Smith *et al.* (1998) showed that although vegetation at some sites could tolerate burning after three year intervals, at least five years without fire was usually necessary to prevent loss of floristic diversity.

In 1965, part of the forest on Mount Carmel, Israel, was designated as a nature reserve and the remainder as a national park, following which forest management practices were neglected in the area so that dead biomass accumulated (Schiller *et al.* 1997). Between 1987 and 1997 fires devastated about 700 ha of the area's unique Aleppo pine (*Pinus halepensis* Mill) forest and in October 1998 another fire destroyed an area of about 250 hectares. Increasing fire frequency may have serious consequences if the seed bank becomes depleted. For example Aleppo pine are obligatory seeders, rather than post-fire re-sprouters like many Mediterranean shrubs and trees (Schiller *et al.* 1997). A fire return interval of less than ten years is therefore a major danger to the regeneration of Aleppo pine forests, since the trees have not yet produced enough seeds for regeneration (Ne'eman *et al.* 1997).

Thus, both grazing and fire at moderate levels play natural and necessary parts in maintaining Mediterranean habitats. However anthropogenic activities can increase the levels of these disturbance types, to a point where there is no longer a balance, and diversity is reduced rather than maintained. Frequent fires, in combination with heavy goat grazing, may result in desertification in a relatively short while (Pantis 1987, PhD thesis in Greek, cited in Petanidou & Ellis 1996). It is therefore important that we discover at what level both fire and grazing and other types of anthropogenic disturbance enhance Mediterranean ecosystems, and at what level there is a risk of losing certain habitats or species altogether. In this way appropriate management strategies can be put into practice where such risks do exist.

1.2 The effects of grazing on fauna

Clearly grazing and fires both affect vegetation, but this must also have knock-on effects on faunal diversity. Very few studies have examined the effects of livestock grazing on other animals in Mediterranean ecosystems. However there have been several studies elsewhere, many concentrating on vertebrates. For example in the Maasai Mara National Reserve (Kenya) the small mammal community was found to be maintained at low densities by the combined effects of grazing and fire, which limited the natural regeneration of woodlands (Salvatori *et al.* 2001). Wales (2001) suggests that grazing of riparian habitats in eastern Oregon and Washington (USA) may affect terrestrial vertebrates by eliminating nesting substrates, altering habitat structure and composition, compacting soil and trampling banks. In Oklahoma (USA), jackrabbits were found to prefer overgrazed areas (Philips 1935; Smith 1940) whereas deer mice and harvest mice were most plentiful in moderately grazed areas, although the total number of small mammal species was greatest in undisturbed areas (Smith 1940). However, of more relevance here are the potential effects on invertebrates.

1.2.1 Arthropods

Grazing has been found to have either positive or negative impacts on arthropods depending on the habitat, the intensity of grazing and the species studied. For example Gibson *et al.* (1992a) studied the effects of grazing on invertebrates on ex-arable grassland and found it to be an advantage to some species like the phytophagous beetle, *Sitona lineatus*, but a disadvantage to others, such as the dipterous leaf miner, *Agromyza frontella* and most of the common Heteroptera.

Positive effects of grazing were found in montane wetlands in Switzerland, where low-density cattle-grazing increased general arthropod diversity (Wettstein & Schmidd 1999). Likewise, grasshopper diversity was found to be encouraged where there was trampling and grazing by cattle in African Savannah (Samways & Kreuzinger 2001) and in the pasturelands of Oklahoma (Smith 1940). Seymour & Dean (1999) also found that in the Succulent Karoo (South Africa), invertebrate abundance was consistently highest under heavy grazing levels.

Conversely though, general arthropod diversity was **decreased** through intensive trampling (by both indigenous game animals and domestic cattle), next to park boundaries in South African Savannah (Rivers-Moore and Samways, 1996) and by overgrazing in Oklahoma (Smith 1940). In northern Victoria (Australia), the ground invertebrate fauna was more diverse in ungrazed woodland than in either grazed woodland or grazed pasture (Bromham *et al.* 1999). Rambo & Faeth (1999) found that insect abundance increased 4-10 fold in ungrazed exclosures in Arizona, but that species richness did not change.

Where grazing intensity has been quantified, studies have found that for some groups intermediate levels of grazing are best. For example in temperate grasslands in New South Wales (Australia), Hutchinson & King (1980) found that abundance of most arthropods was reduced by increased stocking levels, but that numbers of ants increased and Scarabaeid larvae were most abundant at intermediate grazing levels. Seymour and Dean (1999) found the highest diversity of arthropods at moderate grazing levels although abundance was highest in heavily grazed sites. A

Mediterranean study (Verdu *et al.* 2000) on the SE Iberian Peninsula (Font Roja National Park) found that beetles were most diverse in the grassland-shrubland mosaic which existed under controlled grazing activity such as that maintained by traditional methods of sheep and goat herding.

1.2.2 Insect Pollinators

Very few studies of grazing impacts have concentrated on the effects on arthropod pollinator communities and, once more, few studies have been in Mediterranean areas. Those studies that have looked at pollinators again found that grazing had both positive and negative effects. In a study of coastal dunes in the Netherlands, Wallis DeVries *et al.* (2001) found that cattle and pony grazing increased abundance of some open grassland butterfly species. However, grazing effects were not positive for all insect species, although there were no clear negative effects.

1.2.3 Bees

Those few studies making direct links between bee communities and grazing animals have mainly found that the effects of grazing are **negative**. For example Sugden (1984, 1985) suggesed that intensive sheep grazing may be deleterious to bees on pumice flats in California. Gess & Gess (1983) found damage to bee nest sites by livestock trampling in the Succulent Karoo of South Africa. In semi-natural pastures in south-central Sweden, species richness of bumble bees were negatively associated with grazing intensity (Soderstrom *et al.* 2001), and in farmland in the U.K. the sections of transects where most bumblebee visits to flowers were seen were those undisturbed by either cultivation or grazing (Fussell *et al.* 1991).

However none of the above studies were in Mediterranean habitats. Where Mediterranean bee communities have been considered they have suggested the converse effect; that grazing can increase bee populations. For example Petanidou & Ellis (1996) suggested that, in Greek phrygana, grazing may have had positive effects on bees, since its absence led to a uniform shrub layer and a loss of areas of bare ground for nesting. Studies elsewhere have also suggested that grazing may be advantageous to bees; Smith (1940) found that in Oklahoma the numbers of andrenid bees increased enormously when grazing caused grasses to give way to forbs (non-gramminoid herbs) and exposed areas of bare soil for nesting. Carvell (2002) also showed that grazing may be advantageous to bumblebees on Salisbury plain (U.K.); the four most widespread species (*Bombus hortorum, B. terrestris, B. leucorum and B. lapidaris*) were negatively correlated with the amount of moss and grass litter in the vegetation and positively correlated with the number of *Pilosella officinarum* and *Trifolium pratense* flowers and generally high floristic diversity. The habitats that most often had these characters were those recently grazed by cattle.

1.3 Why Study Bees?

Since the majority of phryganic plants are dependent on pollination by insects (Margaris 1984; Herrera 1987), Mediterranean communities are particularly likely to be pollinator-limited (Bond 1994), so any disturbance affecting pollinator communities is liable to have a large impact on the whole habitat. This may be especially important for specialised pollinators (which are dependent on one or few plant species) and for plant species where seed set is pollination-limited, and which only have a restricted number of visitors. In these cases, the loss of plants or pollinators could subsequently cause cascading extinctions throughout the community

(Gess & Gess 1993; Rathke & Jules 1993 and references therein) although this has still to be documented for plant-pollinator communities.

More specifically, Mediterranean areas such as Spain (Herrera 1987), Greece (Petanidou & Vokou 1990), and Israel (Schmida & Dukas 1990) are particularly rich in plants pollinated by bees and the whole of the Mediterranean basin is a known centre of diversity for bee species (Michener 1979; O'Toole 1991; O'Toole & Raw 1991; Petanidou & Ellis 1993). Many plants are fully dependent on wild bees for pollination, and the integrity of the ecosystem may be in peril when the diversity of the bee fauna drops below a critical level (Neff & Simpson 1993). It therefore seems logical to concentrate on bees as study organisms, since any threats to them are likely to have a dramatic effect on the "health" of the whole ecosystem.

1.4 What bees need

The main requirements of bees are sources of pollen and nectar to feed themselves and to provision their nests, as well as materials for building nests and suitable places to situate them (Faegri & Van der Pile 1979; Proctor *et al.* 1996). The other necessity is a suitable climate; insects, due to their small size and proportionally large surface area, are particularly vulnerable to variation in temperature and humidity and these parameters are continually changing due to solar radiation and wind (Willmer 1982). Some bees are relatively adaptable and can make use of a variety of resources (being polylectic) and of habitats, whereas others are extremely specific (i.e. being monolectic); for example, in Greek phrygana, more than one third of bee species were recorded to visit one plant species only (Petanidou & Ellis 1996).

1.4.1 Nesting sites and materials

The nesting requirements of bees are described in detail in O'Toole & Raw (1991). Social bees make complex large nests in natural holes, but in the solitary bees each female has her own nest, and very specific requirements for siting etc. Many species make burrows in the ground and therefore require horizontal areas of bare ground with friable or non-friable soil or vertical banks. Others use plant stems, plant galls, snail shells, sound or rotten wood, old beetle borings and disused cells of other bees and wasps. Many bees ("mason bees") also build exposed nests on the surfaces of rocks or buildings (Photograph 1.1).

Photograph 1.1 Partially built *Chalicodoma siculum* nest at Mitla.

The temperature of the nesting substrate is another important factor (Willmer 1982) since this can affect the rate of egg and larval development (Miyano 1981) and emergence time (Stone 1994). Materials used for cell walls or partitions within the

nest include leaves, petals, plant or animal hairs, plant resin, mud and small pebbles. The requisite materials must be present within reasonable range of a chosen nest site.

1.4.2 Floral rewards

Since bees are almost totally dependent on nectar and pollen as food sources, it seems inevitable that the availability and quality of flowering plants and their rewards must play a major part in structuring bee communities. The diversity of flowers and their rewards have been found to be positively related to the diversity and abundance of bees in set-aside fields in Germany (Gathmann *et al.* 1994), across 14 communities in central California (Moldenke 1975), and in lowland areas of Costa Rica (Heithaus 1974).

The relationship between diversity of bees and that of their resources will also depend on the degree of specialisation in each species. Petanidou & Ellis (1996) found that in a phrygana site near Athens, over a third of bee species were monolectic (recorded visiting only one plant species) and only a minority could be considered generalists. Distributions like this were found in similar habitats in California and Chile as well (Moldenke 1979). On a German salt marsh, grazing by sheep reduced the abundance of *Aster tripolium* so that the plants only flowered in ungrazed areas and flower visitors and pollen feeders depending on this plant became locally extinct (Meyer *et al.* 1995). As mentioned earlier (Section 1.1), situations like this could then lead to cascading extinctions if there were other plants dependent on these pollinators. However monolecty is very hard to prove and, as Moldenke (1979) argues, bees may generalise more when their diversity decreases and therefore not be as specialised as they seem. Even so if it is true that there are large numbers of specialists in phrygana

in Israel, then bee species richness is likely to be closely linked to flower species richness. In contrast, bee abundance is more likely to depend on the total availability of resources, and therefore on overall flower abundance. Assuming that floral reward availability is limiting to bee abundance and diversity, the effects of grazing on bees will be closely linked to its effects on the diversity and abundance of flowers.

1.5 Mechanisms by which grazing animals may affect bee communities.

Livestock-induced disturbance is a composite factor, consisting principally of the effects of defoliation (selective or otherwise), trampling, defecation and urination (Wilson 1990). Sugden (1985) has suggested that this may impose four types of hazard to wild bees in Southern California:

1. Damage to existing nests and broods by trampling
2. Removal of potential nest sites by both trampling and alteration of flora
3. Physical harm to adult bees by trampling
4. Plants are broken and killed by trampling or defoliation, leading to removal of potential food resources for bees.

1.5.1 Trampling

Trampling may affect bees directly when numbers of stock are very high, by destroying nest sites in subterranean burrows, (particularly affecting Andrenidae and Halictidae), or in cavities in hollow stems (affecting Megachilidae). It has also been suggested that male bees may be trodden on when sleeping in flowers (Sugden 1985, Photograph 1.2). However it seems that the risk of this is probably very low unless grazing is extremely intensive.

Less direct effects caused by trampling may also occur such as the alteration of land marks bees use to locate their nests. The number of potential nest sites may also be reduced by caving-in rodent burrows, breaking hollow twigs, or altering the substrate conditions (Sugden 1985). In a study of the effects of grazing on arthropods in eucalyptus forest in Western Australia, various spider species which use permanent burrows and a scorpion which uses the burrows of other species were not present in grazed remnants, probably due to trampling of their burrows (Abensberg-Traun *et al.* 1996); similar effects presumably occur for bees.

Photograph 1.2, Male bees sleeping in a flower of *Cistus salvifolius*.

As well as direct trampling of burrows, the soil can be made harder so that the animals can no longer make their own burrows. Hutchinson *et al.* (1980) found that various arthropod species declined as stocking levels increased in grassland in Australia, and this decline was attributed both to loss of habitat such as litter, and to reduced surface soil pore space, both of which were caused by trampling. An area in Namaqualand in Southern Africa which was previously known as a good collecting area for ground

nesting aculeate species became unproductive in 1993, due to trampling by small sheep and goats which made nesting by ground nesters impossible (Gess & Gess 1993); similar findings were made in another area (Oudtshorn) for the ground nesting sphecid wasp, *Bembix bubalus* (Gess & Gess 1989).

However, several studies have suggested that trampling may also be advantageous to bees, since it opens up areas of bare soil which can be used for nest sites, and also stabilises the soil so that burrows do not crumble. Bees nesting in sandy soils have been found to prefer vegetation-free areas (Wesserling & Tscharntke 1994, article in German, cited in Gathmann & Tscharntke 1994). A decline in bee diversity in Greek phrygana was also attributed to an absence of grazing, resulting in a closed scrub with few bare patches suitable for nesting (Petanidou & Ellis 1996).

Thus bees can be affected by trampling, but these effects may be either positive or negative. Where negative effects have been suggested (e.g. Gess & Gess 1989, 1993), it seems that either grazing was very intensive, or else there was no grazing at all (Petanidou & Ellis 1996). The level of trampling which is damaging to bees may also depend on soil type since some soils (e.g. clay rich soils) will be more easily compacted than others. It therefore seems likely that bees benefit from moderate amounts of trampling since the availability of nesting sites are increased, but that with high numbers of stock, nests and nesting sites are perhaps damaged.

1.5.2 Possible effects of grazing on plant species composition

Both selective and non-selective grazing, or soil disturbance associated with grazer activity, can potentially increase or decrease plant species diversity (Huntly 1991,

McNaughton 1979). However the effect of livestock grazing on flora remains an unresolved and controversial issue. Moderate grazing levels often increase plant diversity, since selective feeding can reduce competition (e.g. for light) from dominant species (e.g. Fahnestock & Knapp 1993). For example in tallgrass prairie in Kansas, some species decreased in number in grazed sites, but in general species diversity was higher in grazed areas (Hartnett *et al.* 1996). Rambo & Faeth (1999) studied pine-grassland communities in Arizona and found higher plant species richness in areas grazed by elk, deer and cattle than in ungrazed exclosures, both in the long-term and in the short-term. The removal of grazers has also been shown to decrease plant diversity; for example the long-term exclusion of large grazers from East African grasslands produced a floristically very poor plant community (Smart *et al.* 1985). However Naveh & Whittaker (1979b) say that long term grazing can have a similar effect to this since it leads to the domination of "undesirable" plant species which are adapted to cope with grazing, and therefore thrive at high grazing levels where other species cannot survive.

It seems likely that floral diversity is indeed increased at certain intensities of grazing but that if grazing is too heavy diversity will decrease again, as a few species become dominant. Those studies which have found either an increase or a decrease in diversity may only have been looking at one end of the scale, i.e. concentrating on either low or high grazing levels. Several studies have specifically shown floral species richness to be higher at intermediate grazing levels than at either high or low levels. For example, in old fields in Virginia, USA, the exclosures with the greatest plant species richness and diversity were those which kept out some of the larger grazing mammals but still allowed some smaller grazers in (Bowers 1993). Gibson &

Brown (1991), studying chalk grasslands in the UK, found that diversity was higher in sheep grazed areas but that it did not increase further when the areas were grazed over long periods. Plant diversity was also found to be highest at intermediate levels in grassland sites in Israel; (Noy-Meir 1995) and in *Quercus* forests in Turkey and California (Naveh & Whittaker 1979a), where a very species rich grass and legume understorey was maintained under moderate grazing pressures, but by under or over-grazing, this was reduced either to unpalatable forbs or to tall aggressive grasses and perennial thistles.

These examples would follow the "intermediate disturbance hypothesis" (Connell 1978). This predicts that at low levels of disturbance the dominant competitors limit or completely eliminate most other species, and that at high disturbance levels all but the most resistant species are excluded. However, at intermediate levels of disturbance, there is a balance between the two. This model has been specifically related to the response of grassland plant communities to grazing by several authors (e.g Grime 1973; Horn 1975; Fox 1979). Two other models have also been suggested to explain the response of grassland plant communities to grazing. Firstly, there is the "predation hypothesis" (Paine 1966, 1971), which suggests that local prey diversity (plants) increases when predators (grazers) prevent dominant species from monopolising resources. The second is the "dynamic equilibrium model" (Huston 1979), which proposes that species richness is a function of the balance between biotic factors (e.g herbivory, parasitism) causing competitive exclusion, and abiotic factors (e.g. extreme climatic conditions) that prevent or delay competitive exclusion.

All these models mean that the highest diversity of plants is likely to occur at intermediate grazing levels. However as noted by Milchunas *et al.* (1988) none of them, when applied to grazing, take into account the fact that the response of a community to grazing depends on its evolutionary history. If an area has a long history of grazing, then many of the species present will be "grazing-adapted", and will therefore be less affected by grazing than those in an area where grazing levels were low previously. As predicted by McIntyre *et al.* (1996), the amplitude of response to a given disturbance should be small for communities where this disturbance has occurred over a long period of time. This was shown by Naveh & Whittaker (1979a) for shrublands and woodlands in Israel. They suggested that, since Israel has been subjected to fairly dense human occupation for over 8000 years, the richness of pastures now represents an accumulation of grazing-adapted species. This means that in Israel, diversity is greatest under very high levels of grazing, which elsewhere (in the United States for example), would be considered very severe and would reduce diversity (cited in Naveh and Whittaker 1979a). At even higher grazing levels however, even in Israel, diversity did decrease again.

It seems likely, therefore, that plant species richness will be highest at intermediate grazing levels in many areas, but that in areas where there is a long history of grazing there may be little or no effect when grazing levels are increased unless they reach extremely high levels. It is also possible that where there is a long history of grazing, its removal may, in itself, act as a disturbance (Milchunas *et al.* 1988) and therefore this may also increase diversity.

All the evidence discussed in this section so far looks at the effects of grazing on the diversity of plant species. However, apart from the need for some nest building materials, the plants that are important to bees will be those which have flowers offering nectar and pollen when the bees are flying. In Mediterranean habitats the flowering season is very short. Almost all plants flower at some time between March and June (Zohary 1962; Auerbach & Schmida 1987; Dafni & O'Toole 1994). This means the diversity of flower types available across this season will probably be closely related to the overall diversity of plant species present. Thus grazing is likely to affect flower diversity in the same way that it affects overall plant diversity. However, grazers may also affect the timing and abundance of flowering in some species, as is discussed in the next section.

1.5.3 Possible effects of grazing on flower abundance

Grazing may increase or decrease the number of flowers produced by certain plant species. For example Bergamier (1998) found that on limestone phrygana in Crete, medium sized and tall grasses and legumes had more flowers when fenced against grazers whereas some low-canopy annuals had fewer. They also found that several annual species flowered earlier in the non-grazed plots than in the grazed plots. Damhoureyeh & Hartnett (1997) found that bison increased flower production in the forb *Baptisia bracteata* in tall grass prairie (Kansas). Noy-Meir & Briske (1996) found that in Israel the proportion of wild wheat plants producing mature inflorescences was 51-59% greater in protected plots than in plots grazed by cattle, but that the number of immature inflorescences was greater in grazed plots. This suggests that the plants in grazed plots attempted to compensate by producing more buds, but that they were eaten before becoming mature. Milton (1994) found that

sheep reduced the flowering of their preferred forage species, in the Arid Karoo of South Africa, but unpalatable species were not affected. Some studies show that grazing animals actually preferentially eat flowers. Anderson (1994) found that deer consumed more *Trillium grandiflorum* plants in flower than not in flower, and that eventually the repeatedly browsed plants did not flower at all. Kirby (2001), in a study of British woodlands, also found that deer often preferentially grazed flowers of several species.

Hence the number of flowers produced by some plant species may be increased by grazing, while in others it may be decreased. Few studies have investigated the effects of grazers on the abundance of flowers across a whole habitat. Increases in plant species diversity (discussed above) may mean that overall flower abundance is increased. At very high levels of grazing, only a few dominant species will remain, as found by Naveh & Whittaker (1979b). However these remaining species are likely to be those that are well adapted to the conditions at high grazing levels and will have little competition since other species are no longer present. They may therefore succeed in producing very large numbers of flowers. Nevertheless, in extremely overgrazed areas there is bound to be a point when almost nothing can survive at all (i.e. a desert) so floral abundance will decline to very low levels. However this situation would only arise where the cattle do not have the option of moving elsewhere or are supplied with additional food. Since cattle can only bite vegetation that is over 5 cm high (Noy-meir *et al.* 1989) the most resilient plants are likely to be destroyed by trampling rather than herbivory.

Based on these studies, floral abundance may be predicted to increase with increasing grazing levels to start with, as diversity increases and as grazing-adapted species become dominant. The greatest abundance will then be reached when only a few species remain, at a higher grazing level than that which is the optimum for diversity. Abundance will then decrease again if extremely high grazing levels are reached, at which point species richness would also be extremely low (Figure 1.1).

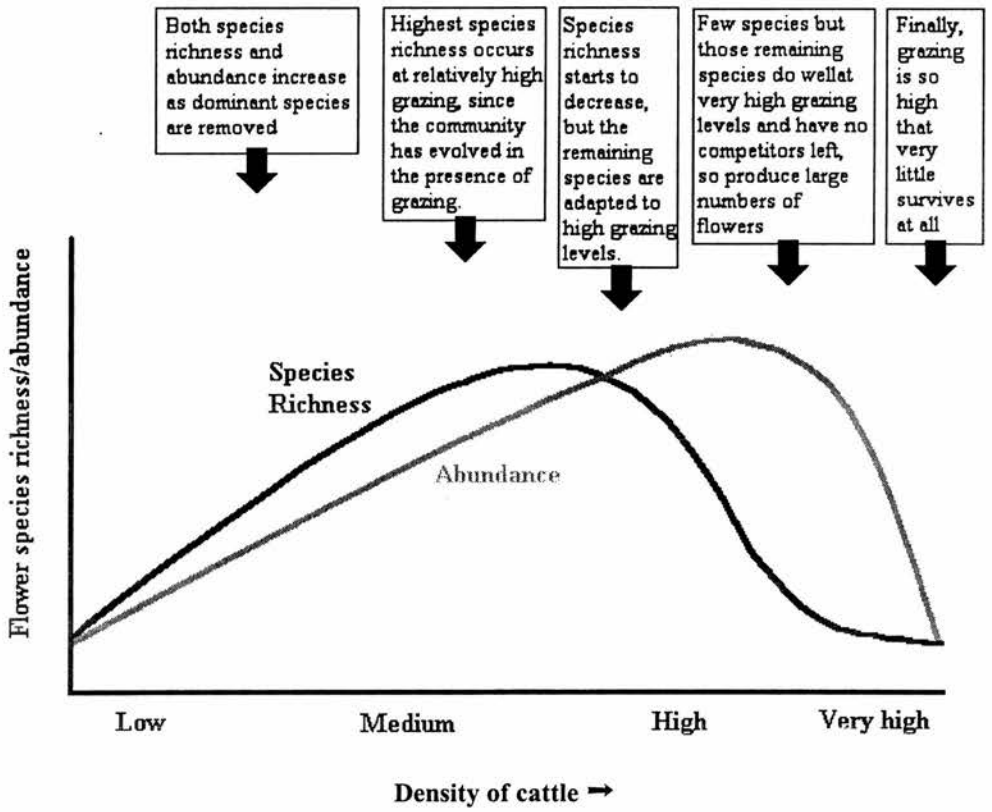


Figure 1.1 Expected changes in floral abundance and species richness with increasing grazing intensity in Israel.

1.5.4 Possible effects of grazing on vegetation structure

1.5.4 a) Microstructure

It has been shown that plants in grazed areas tend to differ in structure from those in ungrazed areas. This happens firstly because grazers select certain plant morphological types, as was shown for goats (Gong *et al.* 1996), and for goats and llamas (Dumont *et al.* 1995). Tall, erect, palatable plants mostly increase with greater

protection from cattle grazing, whereas small prostrate plants and those with low palatability (i.e. those that are grazing-adapted) tend to increase with increasing grazing intensity (Noy-Meir *et al.* 1989; Bowers 1993). Secondly it may happen because a certain plant species may change the way it grows in response to herbivory. For example in grasses, defoliation changes the display of foliage and reproductive parts from taller open arrangements, to compact horizontal positions (Heady 1975) and in many shrubs nodes are closer together when plants have been grazed (MacDonald 1998).

1.5.4 b) Macrostructure

Since herbivores affect the size of many plants rather than their frequency of occurrence, this changes the structure of the habitat (Sala *et al.* 1986). They also graze selectively, reducing the cover of dominant species so that the main effect of cattle grazing may be a horizontal disturbance, opening up gaps in the sward, rather than simply a vertical gradient. This theory was suggested by Grubb (1976) and Grime (1979) and it is also supported by a study of grassland in Israel (Noy-Meir *et al.* 1989) where a protected area had a closed sward of the dominant grasses but a cattle grazed area had open gaps within the sward. Likewise, deKeer *et al.* (1989) and Damahoureyeh *et al.* (1997) found that large herbivores create grasslands with a patchy structure of grazed and ungrazed areas. Grazing has a positive feedback on forage quality since it increases the amount of young re-growth (Wallis DeVries 1996); therefore cattle prefer to return to patches they have previously grazed and this patchy structure is maintained. Consequently, grazing of grass monocultures tends to result in a mosaic of frequently and infrequently grazed areas (Gibb & Ridout 1986, 1988).

The examples above all describe grassland habitats. It has sometimes been shown that grazing plays a part in converting grasslands to shrublands (Milchunas 1993) or reduces herbaceous cover and promotes woody species; for example Madanay & West (1983) found that in Zion National Park (Utah, USA), livestock reduced herbaceous coverage and encouraged the proliferation of woody species. Conversely in Greek phrygana the absence of grazers results in a continuous layer of shrubs, with few open patches (Petanidou and Ellis 1996); therefore it seems likely that in Mediterranean areas, the cover of shrubs is reduced by grazing. This was also supported by Naveh (1982) who found that grazing and browsing in Israel helped to maintain a balance between the different woody and herbaceous strata, and its absence resulted in depleted, one-layered phrygana. If grazing inhibited the growth of shrubs this would create more open areas in the vegetation, producing a patchy vegetation structure, as long as some shrubs were left. At higher grazing levels, shrubs may disappear altogether so that only herbs would be left and vegetation would become more uniform again.

Structural changes in vegetation may be of importance to arthropods. Many butterfly species appear to depend on habitats having a mosaic structure, partly due to their microclimatic requirements (Blink 1997). Dennis *et al.* (1998) found that increased habitat heterogeneity (of both vegetation structure and plant species diversity) was the best predictor of the diversity of small arthropods in indigenous upland grasslands in Scotland. For some species, protection from the weather and from grazers, provided by the tussocks of taller grass left in the more heterogeneous vegetation was important.

For bees, varied habitat structures may be especially important. Woody plants with cavities (such as those created by beetle larvae) are necessary for nesting sites of several species, while areas of bare ground are important for other species. In open areas many species of annual flowers occur, providing diverse rewards. Microclimatic requirements are also important, as for butterflies, and plants have been shown to ameliorate microclimatic conditions (Willmer 1982 and references therein). Variation in plant structure may therefore provide increased variety of microclimates, needed by different bee species. All of these requirements are most likely to be present simultaneously in a patchy habitat.

Bees will also be affected if structural heterogeneity of the habitat alters the numbers of their parasites and predators. For example Gibson *et al.* (1992a) found that large web spinning spiders were sensitive to grazing pressure in chalk grasslands, perhaps because of a lack of structures to attach their webs to. In addition, a more heterogeneous habitat may provide more shelter for birds and other predators. Some bees that nest in cavities created by other animals may suffer a long-term effect if these animals are adversely affected by grazing. For example rodent holes make useful nesting sites for many bees, and rodents need the shelter of scrub patches, which are reduced by grazing (Salvatori *et al.* 2001) as mentioned earlier. Some grassland beetle species were also favoured in areas with little or no grazing (Dennis *et al.* 1997) and if burrowing beetles were similarly affected this may be disadvantageous to bees who could otherwise use their holes.

As was suggested for flowers and for trampling effects, the optimum patchiness for bees is likely to occur at intermediate grazing levels. At low grazing levels, there may be no bare areas of ground for nesting, fewer annual plants, and large amounts of shelter for parasites and predators. However at very high grazing levels, the number of woody plants, and of other animals such as rodents and beetles, may be too low to generate adequate nesting sites and shelter.

1.5.5 Variation in the relationships between grazing and flora

1.5.5.a) Different herbivores have different effects.

Plant choice varies for different grazers. In grasslands, the bite size and intake rate of cattle decline as plant height decreases below 5cm (Noy-Meir *et al.* 1989); therefore cattle are likely to go for the taller species first. However cows are predominantly graminoid feeders (Damahoureyeh & Hartnett 1997) and do not generally choose to feed on woody plants. Dennis *et al.* (1998) found that sheep were very selective on a small scale, leaving close clumps of tussocks in grassland. Cattle however were not sensitive to very small-scale patchiness as sheep were and consequently had a greater impact on the arthropods studied. On the other hand, cattle-grazing on Salisbury plain (U.K.) was shown to be preferable to sheep-grazing for the conservation of bumblebee habitats (Carvell 2002), since cows created a more structurally and floristically diverse sward. This suggests, therefore, that both cattle and sheep increase the structural heterogeneity of vegetation but that they act on different scales, therefore having different effects on different invertebrate species and negative effects on others.

1.5.5.b) Differences in grazing regimes alter the impact of grazing

Herbivory plays different roles in different ecosystems depending on the species of grazer, the intensity of grazing and the disturbance history as described above. Other factors are also important, such as the time of year when herbivory takes place. Noy-Meir & Briske (1996) found that the proportion of plants producing mature inflorescences in Mediterranean grassland was lower within cattle-grazed plots, but particularly when plants were grazed late in the growing season. Plants being grazed at or around peak flowering time may make the most difference to pollinators since the actual inflorescences may be eaten. "Loss of flowers is one of the first effects of grazing, even before the plants themselves have disappeared, and grazing in summer, when the luxurious growth of flowering in spring is over, may have serious effects on the carrying capacity of the system towards bees" (Petanidou and Ellis 1996).

The length of time for which a habitat is grazed can also alter the way it responds to grazing. For example Gibson *et al.* (1991) found that tussock structures (important in maintaining heterogeneity) were retained for one year's grazing but could be lost if grazing continued for longer. A longer period of grazing by a few animals may have similar effects to a short period with large numbers of animals. As suggested by Connell (1978), an intermediate frequency of disturbance or intermediate scale/intensity of disturbance may both lead to highest diversity.

The relative abundance of different plant species also affects feeding behaviour of grazers (Bartolomé *et al.* 1998; MacDonald *et al.* 1998) and some herbivores will resort to feeding on species which they would usually ignore when there is no

alternative (e.g. Augustine *et al.* 1998) or when the preferred forage species are less abundant (Harrington 1982).

1.5.6 Summary of the effects of grazing animals on bee communities

Overall, it seems that the negative effects caused to bees by trampling animals are only likely to be seriously detrimental when grazing is very intensive. At lower levels there may be positive effects, such as the increased availability of possible nesting sites. Trampling at intermediate levels may therefore be a good thing for bees.

The diversity and abundance of flowers is likely to be one of the main factors structuring bee communities, and it has been shown previously that bee diversity and abundance are closely linked to floral diversity and abundance. The effects of grazing on flowers are complex, and depend on many factors, including climate and disturbance history. It is therefore difficult to make predictions about what the effects will be in any one area. However, in general, it seems likely that both flower abundance and flower species richness will reach their highest levels at intermediate grazing intensities, and that the optimum grazing level may be higher for abundance than for species richness as shown in Figure 1.1.

If many bee species are specialists (depending on one or a few flower species) as shown in Greek phrygana (Petanidou and Ellis 1996), then bee species richness and abundance should follow the same pattern as flower species richness and abundance and be highest at intermediate grazing levels. Alternatively it is possible that large quantities of resources may favour one or two bee species and not others, so that dominance develops and species diversity is reduced (Price 1984). In this case

increasing floral abundance may also result in low bee diversity, as one generalist species becomes dominant. However a greater diversity of flowers would still allow more bee species to exist, assuming that at least some are true specialists.

The third important factor to be affected by grazing is vegetation structure. Since the grazers being studied in this project are cattle, it seems likely that taller fast growing plants will be selected out first and that only the shorter and less palatable ones will survive, meaning that overall vegetation height is likely to decrease. Since cattle avoid woody plants (Newman 1993) and do not bite right to ground level as goats do (Harrington *et al.* 1982), it is possible that they do not cause as much damage as goats do in Mediterranean areas and they may therefore increase habitat heterogeneity rather than reducing it. The most heterogeneous vegetation, with a mixture of annuals and perennials, is likely to exist at moderate grazing levels. If a patchy habitat is advantageous to bees, as suggested earlier, then this is yet another factor which may lead to the most diverse bee communities being present in moderately grazed habitats.

The exact level of grazing which leads to the highest bee diversity will depend on where the optimum levels of floral diversity, abundance, and patchiness lie for a particular site, and on the balance between the positive and negative effects of trampling and defoliation.

1.6 Interactions between grazing and fire

Noy-Meir (1995) suggested that, for Mediterranean grasslands, " Fire and grazing should be regarded as two distinct and interactive effects on the community, rather than as two alternative mechanisms of a general disturbance factor." Fire usually acts

on a large scale, resulting in a mosaic of different habitats, which are then made even more heterogeneous by grazing (Petanidou 1999). As mentioned earlier (Section 1.1), fire "re-sets" the vegetation but does not greatly change species composition, whereas grazing is more selective about what it removes and can therefore alter the balance between species. Ne'eman *et al.* (1997) found that during post-fire succession in *Pinus halipensis* forest in Israel, no species replacement took place except for annuals, but the overall plant cover changed. Similar effects were found in *Quercus coccifera garrigue*, in France (Trabaud 1982). Grazing on the other hand is selective, so that if grazing takes place during succession, competition is changed and some species may be selected out, resulting in a more heterogeneous vegetation. Belsky (1992) found that grazing disturbance in Tanzanian grassland had more impact on vegetation cover and diversity than either removal of dominant species or fire. Pantis & Mardiris (1992) found that in lowland pastures in Greece, frequent burning and moderate grazing together led to high diversity but low structural heterogeneity of vegetation.

1.6.1 Grazing changes recovery after fire.

If an area is burned and then left to recover without further disturbance, then eventually it may return to the way it was before the fire as explained above. However, it seems that grazing can slow down this recovery. Mediterranean communities have a much higher number of annual plants in the first few years after a fire than in mature phryganic stages (Naveh 1974, 1990; Moldenke 1976, 1979; Arianoutsou *et al.* 1981). For example in phryganic ecosystems in Greece, during the first years after a fire annuals made up more than 60% of the vegetation cover; 10 years after the fire the vegetation in non-grazed sites had totally recovered whereas in some sites which were grazed, the contribution of annuals was still 60% even 8 years

after fire (Giorgia 1998). This may mean that a more diverse flora is maintained for longer after fire when an area is grazed. The fact that annuals remain for longer may also be an advantage to some bee groups, but a disadvantage to those that rely on perennials. For example, in phrygana near Athens, Andrenidae primarily visit annual plants; while long-tongued bees (such as the Megachilidae) are associated with labiates which are mostly woody perennials (Petanidou & Ellis 1996).

1.6.2 Grazing alters the effects of fire and fire alters the effects of grazing.

Grazing levels before a fire can alter the effects that fire has on the vegetation. Noy-Meir (1995) found that in grasslands, the structural effects of fire were similar to those of cattle grazing, but were greater in ungrazed than grazed grasslands. If the grassland had a strong perennial component and was grazed then species richness increased after fire, but in ungrazed grassland it could go either way. Fire also caused greater increase in bare soil and greater reduction of green cover in ungrazed than in grazed grassland. Collins & Barber (1985) and Collins (1987) found that in North American tall grass prairie, fire increased the species diversity of grazed grasslands but reduced it in ungrazed ones.

Fire can also alter the effects that grazing has. For example in tallgrass prairie in Kansas, bison caused greater increases in species richness and heterogeneity in an annually-burned area than in one burned once, four years before. Mark (1994) found that burning of snow tussock rangelands (New Zealand) could make the dominant grasses more palatable, increasing the nutrient content of the leaves by 82 % so that they were more susceptible to sheep grazing in the following season.

1.6.3 Grazing reduces the chance of fire

Grazing can also reduce the likelihood of repeated fires, as shown by Ne'eman *et al.* (1997), who found a negative relationship between grazing intensity and fire incidence on Mount Carmel, Israel. Perevolotsky *et al.* (1995) found that short periods of heavy cattle grazing kept down woody re-growth along fire breaks for two years and removed biomass and litter that could catch fire. Therefore, although grazing may be detrimental to some habitats, Susmel *et al.* (1976) note that in Italy, removing pastoralists altogether would greatly increase fire hazards.

1.6.4 Summary of the interactions between grazing and fire (Section 1.6)

The predictions made in section 1.5 give a general idea of what the effects of grazing on vegetation may be, but this will probably differ in sites of different post-burn ages. In general, it seems that grazing is likely to slow down the rate of regeneration after a fire and also to decrease the chance of repeated fires. However, since grazing also alters the composition of vegetation, grazing after a fire may mean that an area regenerates to form a different "mature" vegetation than that which existed before the fire. The grazing regime before an area was burned may also have an effect, even if grazing is not continued, since the seed bank will then contain seeds of species which thrived in a grazed habitat.

1.7 Methods of surveying bee communities

Diversity is relatively straightforward to sample when considering static organisms such as plants but for small, mobile animals such as wasps and bees, it is more difficult (Gess and Gess 1993). The possible methods of surveying bee communities

are reviewed by Potts (2002). Those which can be used to measure species richness and abundance across a variety of habitats are listed below.

- **Nest counts.** Nest counts are useful for building up a species list in conjunction with other methods but they make it difficult to provide good information on abundance. This method is also very time consuming and requires experienced fieldworkers with the ability to recognise nests of different bee species.
- **Traps (Malaise traps, window traps, pan traps and sticky traps).** All trapping methods are easy to set up and are good for long-term studies using little manpower, although certain traps may be biased towards certain species. All four types of trap collect specimens that are often wet or damaged and therefore require a lot of handling time before identification. The use of malaise traps and pan traps was attempted at the start of this study, but they were found to be of little use, as discussed in Chapter 3.
- **Working a habitat:** Working a habitat involves sampling as many different habitat components as is achievable in the time available, and this is the best way to get a complete species list. However, there are problems associated with collector bias, repeatability and quantifying sampling effort, so this is not a fair method of comparing different sites or for looking at the relative abundances of different species.
- **Line transects.** Line transects involve walking a set distance at a set speed whilst collecting bees either by sweep netting or by capture/observation. **Sweep netting** has the advantage that many small bees will be caught which may be missed by capture/observation. However, it is impossible in prickly scrub habitats as surveyed in this study, as the net will be caught on bushes.

Capture/observation on the other hand is possible in any vegetation type. It may miss some small bees but it is possible to pursue fast flying ones which may be missed by sweep netting. This method also allows those bees which are seen but missed to be counted or identified in flight. Extensive sampling of large areas can be achieved relatively quickly in this way. Therefore line transects with capture/observation were the main method used in the present study. These were favoured by Banaszak (1980) and are the fairest method when comparing a range of different habitats

1.8 Methods of measuring grazing intensity

The majority of studies on the effects of grazing have used controlled grazing, keeping animals in or out of enclosed areas for measured amounts of time (Cid, *et al.* 1991; Noy-Meir 1990; Bowers 1993; Gibson *et al.* 1992b). This would be the ideal way to quantify grazing intensity since it takes account of what time of year grazing occurs, for how long and by how many animals. One part of this project has used exclosures, to look at the effects on vegetation when grazing pressure is removed. However, this is not practical when looking at a "real life" situation. Nor is it practical when looking at the effects on populations of insects such as bees, which travel long distances and will move in and out of the study area. It is therefore necessary to find out what the existing grazing levels in the area are. Various methods have been used where controlled experiments were not possible.

- **Spoor counts**

Spoor counts have been used as indices of large carnivore populations by Stander (1998) and showed a linear correlation with true density (though this study was

done with tracked animals, meaning that a large proportion of the spoor would have been found). Faeces have also been used as an index of recent grazing intensity for geese (Gauthier *et al.* 1995), sheep (Arnold 1995; Abensberg-Traun 1996) and, in combination with trampling and vegetation structure, for cattle and ponies (Wallis DeVries 2001). This is a relatively simple way to measure grazing intensity, but depending on how long faeces last, it may only provide information on very recent grazing. There may also be problems due to some animals having "latrine" areas, so that the areas where the most dung is found are not necessarily where the animals spend most of their time (Wallis DeVries 2001).

- **Known history**

Information about grazing history has been obtained from information on the granting of grazing permits (Giorgia *et al.* 1998), and from the local shepherds (Pantis & Mardiras 1992). This is useful to find out grazing levels on a large scale, and may often be the only way to find out about grazing that was not very recent. However, animals may choose to feed in certain small areas more than others, and it is unlikely that farmers will have observed them closely enough to have information on exactly which areas are most heavily used.

- **Bitten stems and node lengths**

Bowers (1993) used the number of bitten stems to record the grazing levels on any one plant species. Another method which can be used on some shrubs is to measure node lengths. Nodes will be closer together when plants have been grazed (MacDonald 1998). Pantis & Mardiris (1992) used the mean heights of woody plant species to determine grazing pressure, since McNaughton (1979,

1984) and Wojterski (1990), among others, showed that increasing grazing pressure decreases the mean height of woody species. However, all of these methods are dependent on the presence of the same plant species across different sites, and would therefore be impractical when comparing sites with quite different vegetation types. The measurements of node lengths and of vegetation height are also dependent on shrub species being grazed, yet it has been shown that cows prefer to feed on graminoids and do not generally choose to eat shrubs (Damahoureyeh & Hartnett 1997) unless there is no other choice. There may therefore be no obvious effect of cattle grazing on node lengths or vegetation height where herbs and grasses are abundant.

- **Indicator species**

Other possibilities include finding species which are specific to grazed areas, such as grazing-adapted plants or possibly dung-feeding invertebrates or ungulate parasites. For example the height of White Flowering Trillium (*Trillium grandiflorum*) has been used as a useful indicator of deer browsing intensity (Anderson 1994). However, once again, this would not be useful when comparing very different habitats, such as freshly burned sites and mature forests, since many other factors may also influence the abundance of these species.

- **Soil analysis**

Grazing and disturbance by rabbits and ungulates results in changes in soil composition and structure (Saunders & Hobbs 1992). Powell *et al.* (1998) found that the addition of sheep urine to sandy, silicaceous soil increased pH, phosphorus and ammonium levels dramatically in the upper 10-15 cm of soil,

especially during the first week after application. It may be possible to use soil analysis to determine the presence of grazers. However there are so many other variables affecting soil composition that it would be necessary to take huge numbers of samples, and again it would be difficult to compare sites of different ages.

1.9 Study area

The main area studied during this project was Mount Carmel National Reserve in Northern Israel. This area was chosen since Israeli habitats are known to be global hotspots for bee diversity (Michener 1979). The whole of Israel has 1500 to 2000 known species of bee, and Mount Carmel alone has at least 600 to 700 species (O'Toole and Raw 1991). The Mount Carmel area is one of few small areas of Mediterranean habitat within Israel and has many unique flower species. It also includes the largest natural forest of the genetically defined East Mediterranean Aleppo pine group (Schiller *et al.* 1997). The region is currently experiencing increasing risks from wildfires (Kliot & Keidar 1992) and there is also heavy grazing in some parts of the reserve. Hence the vegetation on Mount Carmel consists of a mosaic of habitats at different stages of regeneration. Within these areas, the varying levels of grazing have acted on a smaller scale, making the vegetation even more heterogeneous. In the past the grazing in the area has been mainly by goats, but in recent years goats have been disappearing from the rangelands (Seligman & Perevolotsky 1994) and many farmers have gone over to cattle production (Eli Sandovski, pers. comm.). It is known that overgrazing by goats has caused much damage to Mediterranean habitats in some areas (Petanidou & Ellis 1996; Perevolotsky *et al.* 1998); however the feeding preferences of cattle and goats differ.

Goats tend to eat more woody plants than cattle do (Harrington 1982) and avoid graminoids (Bartolomé *et al.* 1998) and therefore have quite different effects on their environments.

1.10 Aims of this project

This study took place as a "tied" studentship, and therefore happened in conjunction with another project: "Threats to biodiversity of Mediterranean plant-pollinator communities; effectiveness of pollinator guilds and plant reproduction under intensifying wildfires, agriculture and introduced bees". The main project aimed "*to assess the impact of various disturbance regimes on the composition of bee assemblages and on their relative effectiveness as pollinators in a range of Mediterranean habitats; and to identify possible long-term ecological consequences, and hence conservation needs, for disturbed plant-pollinator communities*". This meant that some of my time was spent collecting large quantities of data in the field, in conjunction with Dr Simon Potts, Prof Pat Willmer and others, which is not all included in this thesis. It also meant that the surveys took place across sites which had more variation in post-fire age than might have been ideal for a study of grazing effects alone.

In this thesis, I have focused particularly on the effects that grazing cattle have had on the recovery of the plant-bee communities in these areas after fires. The ecosystem being studied is composed of a highly diverse flora which is almost exclusively pollinated by bees and the primary objective is to discover what the effects of grazing levels on the bee communities are, in sites of varying post-burn ages. I then aim to explain how these effects come about, through changes in habitat parameters such as

floral diversity and abundance, energy availability (pollen and nectar), and vegetation structure. It will then be possible to assess whether the present grazing regimes are having positive or negative effects on the bee community, and why, and therefore whether any changes in management strategies are needed.

2 Study Sites and Methods

Data were collected over three field seasons. The main study was based on Mount Carmel in Northern Israel. Around 4 months (February to May) in each of 2 years (1999 and 2000) were spent in this site. Initially it was planned to spend a third season in the same area of Israel in 2001. However the political situation meant that we were unable to return there. Instead, related studies were carried out on the Island of Lesvos, in Greece during spring 2001. This site was chosen because it had areas with a similar habitat types to those on Mount Carmel, in addition to several extensively burnt areas. Also, collaboration with Dr Theodora Petanidou, of the University of the Agean (Based in Mytilini, Lesvos) and her knowledge of the area made it possible to quickly find suitable field sites.

Initially, I had hoped to continue with very similar studies to those carried out in Israel, particularly concentrating on cattle grazing effects in intermediate aged phrygana. I also wanted to investigate in more detail, the effects of "edginess" caused by grazing and of exclosures, floral structure, rewards, and visitation. However, it turned out that most cattle in Lesvos were kept on improved grasslands, therefore related studies were carried out, looking at goat grazing/browsing rather than cattle grazing.

The methods for the whole study are described in this chapter and are split into four main sections. First I describe the methods used for the main study of the effects of grazing on pollinators in Israel. I then give the methods for a study on edginess and patchiness (as created by grazers) and its effects on floral rewards in Lesvos, followed

by a study of the effects of goat grazing on flora in Lesvos. Lastly, I describe experiments using exclosures in both Israel and Lesvos.

2.1 Grazing and pollinators in Israel

2.1.1 Study sites in Israel

The main part of this study took place in Mount Carmel National Reserve in Northern Israel from late February to mid-May 1999 and 2000. The area consists of a mosaic of different aged areas of post-fire vegetation . Mature (maquis) areas are made up mainly of *Pinus halipensis* forest and also some *Quercus calliprinos* forest. The intermediate aged phrygana is dominated by *Cistus salvifolia, Cistus creticus, Calycotoma villosa, Pistacea lentiscus and Sarcopterium spinosa* which also form an under storey in mature areas. However there are also more recently burnt areas, which are covered with grasses and annuals, even a few months after a fire. The largest recorded fires within the area took place in 1998 (in two different areas), 1989, 1985 and 1974. General characteristics of these burnt areas are shown in Table 2.1. The positions of the burnt areas and examples are shown in photographs 2.3 to 2.9 at the end of this chapter.

As well as varied ages of vegetation the whole area is subject to varying levels of grazing. In the past this has been mainly by goats, but in the last ten years many farmers have gone over to cattle production. All the sites used in this study were grazed by cattle or not at all. The animals are generally herded through the area rather than being enclosed in one place. Further details of this are given in the questionnaire results in Chapter 4.

Sites were selected to represent a variety of ages and of grazing levels. The position of each site was recorded using a hand held GPS (GARMIN OLATHE, KS. USA). Seven main sites on Mount Carmel were examined in 1999, two in separate areas burnt in 1998, two over 50 years old (hereafter referred to as mature) and one in each of the areas burnt in 1974, 1983 and 1989 (listed in table 2.1). Each site had an area of at least 1 hectare and was at least 0.6 km from any others. Within each site, three sub-plots were selected which were typical of the site and were at least 100m apart. Sites were selected to have slopes, aspects and soil types as similar as possible to one another. The slope of each plot was measured by calculating the mean of inclinometer readings in 5 different places and aspects were recorded using a compass. Altitudes of the sites were taken from maps. Soil types were taken from Soffer and Kipnis (1980). All aspects, slopes and soil types are shown in Table 2.1.

During the 2000 season, repeat surveys were made in all these same sites apart from DenNB (a mature site) which burnt down in December 1999. At the start of the second season, a new site (NewNB) was selected of the same burn age as DenNB. A second site within one of the freshly burnt areas (Hod Repeat) was selected in order to give more variation in grazing levels and part way through the season two additional sites in the 1983 burn were also included (Mit Shed and Mit Bot) which had higher grazing levels than the original sites and a better known history. Since these sites were only found after fieldwork had begun, they could only be surveyed from mid March until May. Surveys of the rest of the sites were carried out during the main bee and flowering season (February to May) each year, with the peak of both bee and flower abundance occurring in early April. All survey times are shown in Table 2.1.

A full survey of the all three plots within one site took a full day. A full round of all

the sites was completed 5 times within the season, the survey days in each round, being kept as close together as possible. This was dependant on weather, but usually a whole round was completed in less than 26 days. The extra sites, Mit Shed and Mit Bot were only surveyed during the last three rounds in 2000. Temperature and humidity were recorded throughout each day using a hand held meter (HMI 31, Vaisala, Finland). Any days with particularly abnormal weather (e.g. rain or high winds) were discarded and repeated the following day, since many bees would be unable to fly in these conditions and nectar and pollen production would also be affected.

One day's survey of one site included measures of :

- Grazing levels
- Bee diversity and abundance
- Flower diversity and abundance
- Nectar and pollen rewards
- Vegetation structural heterogeneity
- Soil hardness
- Soil nutrients (nitrogen, phosphorous and pH), were also measured in each plot at the end of the season.

All these methods are given in the following sections.

Site name	Den	Hod	HodRep	Hai	Mit	MitBot	MitShed	Etz74	EtzNB	DenNB	NewNB
year burnt	1998	1998	1998	1989	1983	1983	1983	1974	<1950	<1950	<1950
Location	Wadi Denia	En Hod	En Hod	Haibar reserve	Mitla	Mitla	Mitla	Etzbah	Etzbah	Wadi Denia	Kedumim
Time surveyed	Whole season. 1999 and 2000	Whole season 1999 and 2000	Whole season 2000	Whole season 1999 and 2000	Whole season. 1999 and 2000	March to June 2000	March to June 2000	Whole season 1999 and 2000	Whole season 1999 and 2000	Whole season 1999	Whole season 2000
Estimated grazing level	Very low	High	High	None	High	Very high	Very high	None	Very low	None	None
Approximate burn area (ha)	100	450	450	300	400	400	400	80	240	190	135
GPS	32°45.8' 35°00.1'	32°41.9', 34°58.6'	32°41.7' 34°59.0'	32°44.9', 35°01.2'	32°44.2', 34°59.6'	32°43.4' 34°59.05'	32°44.2' 34°59.1'	32°42.4', 34°58.9'	32°42.4', 34°58.8'	32°45.7', 35°00.4'	32°43.3', 35°04.2'
Altitude a.s.l (m)	290	130	150	320	340	220	210	180	170	320	290
Aspect (°)	247-286	298-320	220	233-296	216-327	240-250	270-290	143-187	178-247	186-251	172-234
Slope (°)	9-17	5-7	10	1-4	5-12	5-12	3-5	4-15	5-9	12-13	6-13
Mean annual rainfall (mm)	675	625	625	725	675	675	675	625	625	700	650
Soil type	Terra Rossa A1	Terra Rossa A1	Terra Rossa A1	Rendzina, C1	Terra Rossa A2	Terra Rossa A2	Terra Rossa A2	Terra Rossa A1	Terra Rossa A1	Terra Rossa A1	Terra Rossa A1

Table 2. 1. Physical characteristics of survey sites on Mount Carmel. Soil type and mean annual rainfall are from Soffer and Kipnis (1980). Terra Rossa A1=Red; non or slightly calcareous; developed from limestone or dolomite; Terra Rossa A2=Brown-Red; slightly or moderately calcareous; mainly developed from limestone or dolomite; Rendzina C1=Light brown; moderately calcareous or calcareous; developed from hard chalk or poorly developed nari.

2.1.2 Grazing levels

Several possible ways of assessing grazing levels were discussed in Chapter 1 (Section1.4). However those methods which were most practical in this situation were to use dung counts, and to back this up with information from the local farmers. An experiment was also performed to try to use dung density to determine the age of dung samples and to discover how long cow dung remains before degradation in this habitat (described in section 2.1.2 c).

2.1.2 a) Questionnaires

At the most intensively grazed sites (three at Mitla 1983 burn and two at Ein Hod 1998 burn) farmers were given the following questionnaire (also translated into Arabic) to find out the basic history of the sites. This could not be done at other sites since they were very irregularly and infrequently grazed and it was not possible to trace the farmers.

Grazing Questionnaire

1. For how many years have animals been grazed in this area?
2. For how many months each year are they grazed?
3. Have the animals always been cattle or have sheep or goats been grazed here?
4. How many animals are usually grazed here at one time?
5. Are the animals herded through the area or kept here permanently?
6. Was any of the area cleared before grazing began?

2.1.2 b) Dung counts

A 50m tape was laid out in each plot always starting from an accessible point, usually close to a track. One person spun round with their eyes shut and threw a stone, then

walked in a straight line in that direction until the tape ran out. The total number of cow dung pats was recorded in a 1m wide strip along each side of the tape. Dung from other species was also noted but since their occurrence was extremely low, this was not included in the analysis. In 1999 each dung pat was weighed using kitchen scales, and the volume calculated by measuring the mean diameter and depth of the sample (as in Section 2.1.2 c), but where the samples were spread out or broken up they were collected together in a beaker, so that volume could be estimated. Results of dung decay experiments were to be used to try to calculate the age of each dung sample from its density; however this turned out not to be possible (see dung decay experiments) so in 2000 dung samples were simply counted. Dung was counted each time a site was surveyed and another 5 times at the end of the season, giving ten transects for each site in total.

2.1.2 c) Dung decay experiments

Dung decay experiment A: In April 1999, ten fresh cow pats (those that were still wet, and estimated to be 1-3 days old) of varying sizes were moved onto sheets of chicken wire and marked. They were grouped in one part of the grazed area so that they could easily be found again. They were weighed and their volumes were calculated every 7-10 days (5 times in total). To estimate volume, the diameter of the cow pat was measured at ten points across the top then depth was measured by inserting a narrow spike with measurements on, at ten random points. The mean diameter and depth were then used to calculate volume, treating the cowpat as a flat cylinder.

Graphs of weight/volume against time were plotted to ascertain whether density could be used to estimate the ages of dung samples found on transects. The samples should have been measured again in the autumn but had been heavily trampled by cattle and labels lost. Some cowpats were still present a year later showing that dung could last at least a year. However plants had grown up under the wire, holding the dung pats up off the ground so that they may have been kept much drier than average and may therefore have decayed more slowly.

Dung decay experiment B: In April 2000, cow pats were marked *in situ* Photograph 2.1) to investigate whether they naturally last more than 1 year, when on the ground rather than on chicken wire, and also to test whether decay rates were similar across different sites.

Photograph 2. 1 A marked cowpat at Mitla.

Ten cowpats were marked at Mitla and ten at Mit shed. The percentage of these still present was recorded on leaving Israel in May 2000. This should have been recorded again in February 2001; however it was not possible to return to Israel at this time due to the political situation. In February 2002, S. Potts recorded that a small amount of dung still remained, but some samples were not found and some had again been trampled by cattle.

2.1.3 Bee surveys

Various methods of measuring bee diversity and abundance are discussed in Chapter 1. For this survey the main method used was to walk transects, set up each day, whilst counting and catching as many bees as possible using an insect net as described below. Initially, focal plants were also watched for fixed time periods. However, due to the patchy distribution of flowers, it was not possible to watch one patch that was typical of the whole habitat and the same flower species were not present across all habitats. There was therefore no way to employ this technique fairly, across all sites.

The use of malaise traps was also attempted initially. However very few specimens were caught and the majority were flies rather than bees. Pan traps were also tried using yellow, since this has been shown to be the most effective colour for Hymenoptera and flies (Dafni *et al.* 1990). However, most bees caught in these were of the same species, while what was recorded along transects was relatively diverse. The use of these traps would therefore have biased our measures of species abundance and added little to measures of species richness.

Bee transects involved a fieldworker walking 100m in one direction, over 10 minutes and counting all bees seen within a 1.5m, on either side and above them. As many bees as possible were caught using an insect net. If easily identifiable the bees were released; otherwise they were killed, using a killing jar containing ethyl acetate and pinned for identification later. These transects were walked at 7:00, 10:00 and 14:00 on each survey day, which covered the period of maximum bee activity (initially a further survey was done at 17:00, but very few bees were seen at this time). Two transects were made in each plot at each survey time. In 1999 the same two people simultaneously walked 10 minute transects in each plot, giving a total of three man hours a day for each study site. In 2000, fieldworkers varied and only one fieldworker was available to catch bees on most days, so two ten minute surveys were done in each plot, spread as evenly as possible across time, i.e. surveying plots 1,2,3 then 3,2,1, still giving a total of 3 man hours per day. During the second season, more bees were released since more could be identified by then.

Totals were also counted for those bees which could be identified on the wing: *Bombus terrestris*, *Apis mellifera*, *Habropoda tarsata* and *Andrena pyropygea*. All pinned bees were taken to Oxford University Museum of Natural History for identification by Chris O'Toole (Head of the Bee Systematics unit).

Bee abundance was calculated for comparative purposes, as the total number of bees seen in a plot across the whole season. Diversity was calculated as the total number of species recorded across the season. These were calculated for all 5 rounds of data in both years. Separate calculations were also made for the last three rounds only in 2000, so that the sites only measured for the second half of the season would be comparable. Bee species lists are given in appendices 1 and 2.

2.1.4 Floral surveys

The 50m transect used for dung counts (2.1.2 b) was also used for floral surveys. The species in a 20cm band on either side of the 50m tape were identified. The number of flowers of each species was counted and the average diameter was estimated for each species. For any one species, the number of flowers, multiplied by the estimated diameter, was used as an estimate of flower cover. Although this was an inaccurate measure in many ways, it was sufficient for comparisons of relative abundances across sites. Only open flowers, likely to have nectar or pollen available to bees, were recorded.

A reference collection of pressed flowers was also kept when a specimen could not be identified immediately, and identifications were made using Blamey and Grey-Wilson, (1993) and Zohary M (1996), and with the help of Prof. A. Dafni and Dr T. Riano-Rodrigez (Haifa University), Prof. P. Willmer (University of St. Andrews) and Mr R. Vulliamy. Flower species lists are given in appendices 3 and 4.

2.1.5 Floral rewards

2.1.5 a) Bagged and unbagged flowers

Flowers were bagged in each plot, either the evening before a survey or very early on the morning of the survey, prior to the onset of flower visitor activity. Areas were selected for bagging by following a random transect and placing a $1m^2$ quadrat every 5m. The first three quadrats containing flowers with measurable nectar rewards were covered with fine netting to prevent access to visitors. Sampling continued until three bagged quadrats had been set up or until ten quadrats had been tried. The number of empty quadrats was also recorded. Flowers were bagged if they were open or if there

were buds likely to open on the survey day. The same was done for flowers with pollen rewards.

For nectar sampling, flowers in the area outside the nets were used as well as inside. Readings were taken from the same species of flowers in the same numbers as were present in the bagged quadrats. Nectar from inside the bags was used to give a measure of the nectar standing crop, without visitation (maximum producible nectar) and that from outside gave a measure of the nectar standing crop with open visitation (actually available nectar).

2.1.5 b) Nectar measurements

Nectar volumes were measured between 11:00 and 12:00 since at this time, the majority of flowers had opened, yet few had died. Some flowers (e.g. *Cichorium pumilium* and some *Geranium and Erodium spp.*) were already dead by this time towards the end of the season, when temperatures were high. Also, the peak time for nectar production varies between species. However, since measurements were taken at the same time each day, they were adequate for comparison across sites.

Samples were taken by carefully inserting micro-capillary tubes (Camlab, UK, 0.5 to 10µl, as appropriate) into the flowers to draw nectar out of them. For labiates, the flowers were gently pulled out of their corollas and squeezed, so that a drop of nectar formed at the flower base, which could be collected into a micro-capillary. Volumes were assessed by measuring the length of the column of nectar in the tube. Concentrations of these samples were measured using sugar refractometers (0-50% and 45-80%) modified for small volumes (Bellingham and Stanley, UK).

As many flowers were sampled as necessary to obtain a mean concentration and volume reading for each species in the quadrat, and the total number of flowers of each species in the quadrat was counted. Nectar measurements were also taken for the same number of flowers of the same species from the surrounding habitat. Where there were very few flowers in a quadrat, extra flowers of the same species were bagged so that there were enough to obtain a reading. On some occasions flowers contained so little nectar that all the flowers bagged did not give enough nectar to obtain a concentration reading. In these cases, the average concentration for that species in the same site was used.

2.1.5 c) Nectar energy

The results from Section 2.1.5 b, were used to calculate the total energy availability from nectar, in Joules m^{-2}, in each plot. The mass of sugar available in each sample, and then the total energy content, were calculated using the formulas from Dafni (1992):

$$\text{Milligrams of sugar in sample} = \frac{\%\ \text{sugar}}{100} \times \text{volume of sample in } \mu l \times \text{Density of sucrose at the observed concentration.}$$

1 mg sugar (sucrose) = 16.8 Joules

and tables for conversion of sucrose concentrations to density, also given in Dafni (1992).

2.1.5 d) Pollen sampling

Pollen was sampled by clipping the anthers from all flower species in the second set of netted quadrats, as long as the flowers were open. When a lot of pollen had fallen

onto other flower parts, they were also included. These flower parts were preserved in 70% alcohol to return to the UK. Where there were few flowers all of them were sampled and pollen from all species preserved together in one vial. Where there were too many flowers for all of them to be sampled, pollen from at least ten of each species was collected. In this case, pollen form each species was kept in a separate vial. The total number of each flower species in the quadrat was counted so that later it was possible to calculate the total amount of pollen available in each quadrat.

2.1.5 e) Pollen counting

The samples were sonicated for 5 minutes to release all the pollen from the open anthers (including poricidal anthers, which normally require buzz-pollination) then filtered through a net, to remove coarse floral debris but let pollen through. Closed anthers were not opened since the pollen contained in these was not available to bees at the time of sampling. Four methods were tested for measuring pollen biomass.

1. The volume of each sample was measured in a calibrated vial, and grain numbers in two sub-samples of 0.9 µl, were counted using a haemocytometer (Weber Scientific international Ltd) as suggested by Dafni (1992). Pollen counts using this method appeared to be very low which may have been because 0.9µl was such a small sub sample from suspensions of up to 14ml. Also, when using a haemocytometer, the sample is added to the well, under the edge of the coverslip which has been pressed onto the slide to form a seal. Some larger pollen grains seemed to be caught at the edge of the coverslip and not get underneath and into the well and therefore were not counted.

2. The volume of each sample was measured as above. Two 20µl sub-samples were taken from each tube and the number of grains counted in 50 fields of view on ×30 magnification, under a coverslip. The area of a field was measured using a stage graticle (Graticles Ltd, Tonbridge, Kent) and the total area of the coverslip using an eyepiece graticle. The total number of pollen grains in 20µl and then the total number in the tube could then be calculated. The first 30 pollen grains in each sample were measured and the average volume of a grain calculated (as explained below), to give a total volume of pollen per m^2 in the plot. This was done for all the samples collected in 1999. When samples were sieved, the floral debris were rinsed through with alcohol, therefore some samples became very dilute. This meant that some sub-samples were still a very small proportion of the total sample and many were very variable or had very few pollen grains. This method was improved in 2000 by concentrating the samples as below.

3. All the samples collected in year 2000 were centrifuged after sonication until the pollen formed a pellet at the bottom of the tube. The liquid was then poured off and the pollen re-diluted to exactly 100µl. Grains were then counted in two 20µl sub-samples as above. This method gave better accuracy than the previous one since very few samples were found with no pollen at all.

4. A fourth method was tried, to calculate the weight of the pollen samples instead of the volume. Filter papers were dried overnight and weighed, then pollen samples were filtered through them. The papers were then dried again and re-weighed and the total weight of the pollen calculated. However dust,

cell contents and other debris were collected on the paper as well as pollen leading to inaccuracies.

2.1.5 f) Pollen volume.

The first 30 pollen grains found in each sample were measured under X 60, using an eye piece graticle. Almost all pollen grains were either spherical or elliptical so the diameter of each pollen grain was measured at the longest point and perpendicular to it using an eye piece graticle. In order to estimate grain volume, an elliptical pollen grains was treated as a cylinder with a half sphere on each end, as in Figure 2.1.

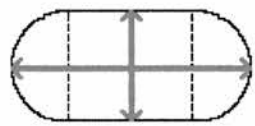


Figure 2. 1 An elliptical pollen grain, shown as a cylinder and two half spheres. Arrows show measurements taken.

The volume of each measured pollen grain was calculated and used to obtain a mean grain volume for each sample. These values were then used to calculate the total volume of pollen per m^2 in each plot.

It was later found that there was still some inaccuracy in these methods since pollen grains of some species, such as *Cistus creticus*, appeared larger when under a coverslip than those without a coverslip. The coverslip squashed the pollen grains slightly (Figure 2.2), so that the grain diameter was greater when viewed from above, hence pollen volumes for some species will have been slightly overestimated.

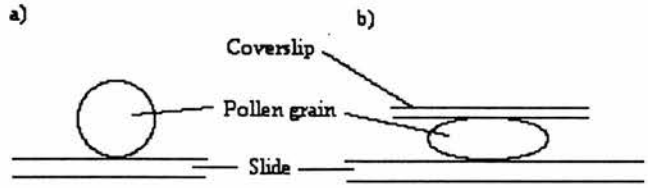


Figure 2.2 Cross section of *Cistus creticus* pollen grain, a) without a coverslip and b) with a coverslip.

2.1.5 g) Pollen energy

Pollen volumes were used to calculate the total availability of energy from pollen per m^2 of habitat. Pollen mass was estimated using a regression equation relating pollen grain mass to volume ($\ln [mass] = 0.95 \times \ln [volume \times 10^{-6}] - 12.46$), presented in Roulston, Cane and Buchmann (2000). For a value of pollen energy per unit mass, a mean (5.7 Kcal g^{-1}) from 34 insect pollinated plants in a similar Mediterranean ecosystem (Petanidou pers comm.; Petanidou and Vokou 1990) was used. 1 Kcal = 4186 joules so this is equal to 23860 Joules g^{-1}. These values together were then used to calculate pollen energy content per m^2 for each plot.

2.1.6 Structural heterogeneity

In 2000, vegetation heterogeneity was measured in detail along the same 50m transects as were used for floral surveys and dung counts. Vegetation height (to the nearest 10cm) was measured at points at 1m intervals along the tape and presence or absence of trees shading each point was recorded. Anything over 3m high was counted as a tree.

2.1.7 Soil

Twice during each season 5 quadrats were randomly placed in each plot. Ground hardness was measured using a penetrometer (E.L.E. UK. Ltd), measuring the

pressure needed to push it 5mm into the soil. This was done at ten points in each quadrat. Readings were categorised as hard (>4 Kg cm^{-2}),medium (2-4 Kg cm^{-2}) and soft (<2 Kg cm^{-2}) and the proportion of each was recorded.

Soil samples were taken from each plot by removing the top 5 cm of soil and taking 10 cm^3 from below this. Three samples were taken within each plot and pooled. Nitrogen, phosphorus and pH levels were tested using a Westminster soil testing kit (West meters Ltd).

2.2 Grazing and pollinators in Lesvos: Effects of edges on floral rewards and visitation in Lavandula stoechas and Cistus creticus.

2.2.1 Study Sites in Lesvos

Fieldwork in 2001 took place during April and May on the Island of Lesvos in the East of the Aegean Sea, close to Turkey. The study sites were on the South Coast of the island, close to the village of Vatera and on the East side of Kalloni Gulf, near to Aschlederi. The area was mostly limestone, covered with phrygana and *Pinus brutia* forests, a lot of which were heavily grazed by goats. Dominant shrub species in the phrygana were *Cistus creticus, Cistus salvifolia, Quercus coccifera* and *Olea europea oleaster.*

2.2.2 General methods for edginess study

Two plant species were chosen which occurred both within thick scrub and on the edges of scrub patches. The plants chosen were *Lavandula stoechas* and *Cistus creticus,* as they were both flowering in adequate numbers during the study season.

Study sites were chosen where the habitat was "patchy", meaning that there were scrub areas with open areas in between as shown in Photographs 2.2 a and b.

a)

b)

Photograph 2. 2 a) Patchy habitat, b) thick scrub at Aschlederi, *L. stoechas* study site.

A plant with at least one side facing an open area of at least 4 m^2 was counted as "edge". Anything at least 2m away from all edges was counted as "centre" as shown in Figure 2.3.

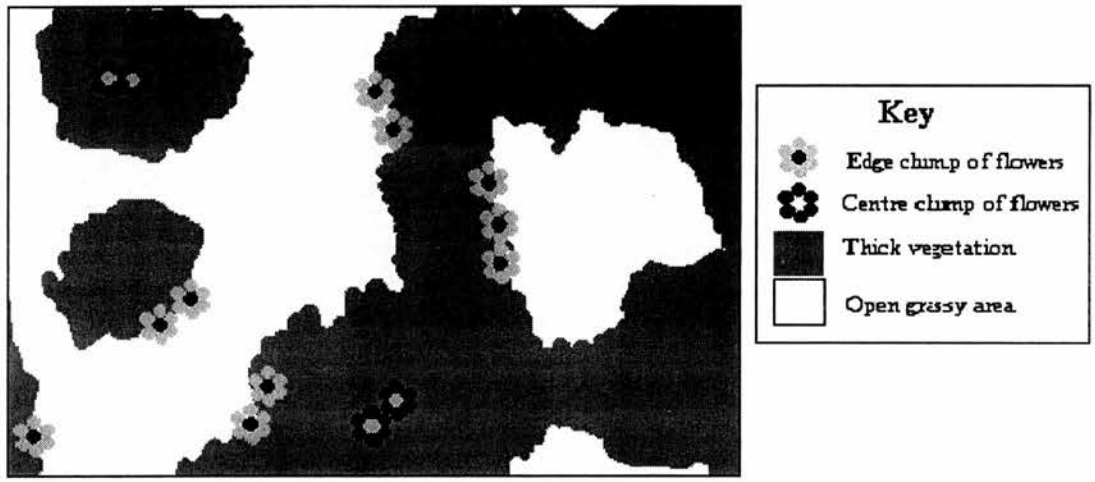


Figure 2. 3 Showing flowers clumps in "edge" and "centre" areas.

2.2.3 *Lavandula stoechas* study

This study took place in an area of phrygana, burnt in 1977 (24 years ago), close to Aschlederi (GPS lat. & long.: 26°16.8', 39°09.4'). *Lavandula stoechas* grew in dense clumps, with flowers born on short spikes with conspicuous bracts (flags) as in Figure 2.4. On five days, as close together as weather allowed, recordings were made of nectar production and visitation to *L. stoechas* clumps in centre patches and on edges of patches. The mean number of flowers per spike was recorded for each of the watched clumps on three of these days. Plant density, mean number of spikes per plant, mean number of plants per clump, clump size and seed set were also recorded in each area. Temperature and humidity were measured throughout the day for those days when nectar and visitation were recorded and any days where these were very different from average were discarded.

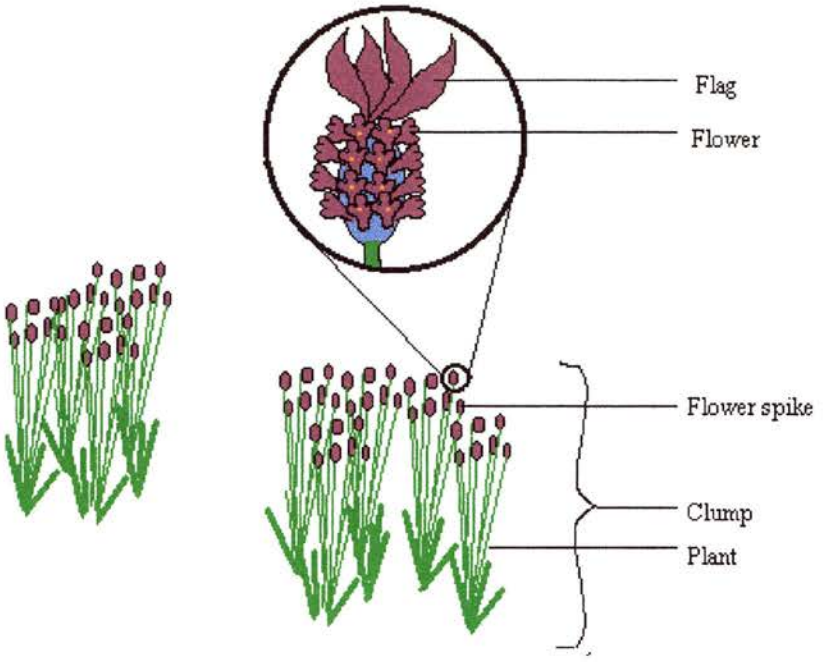


Figure 2.4 A clump of *Lavandula stoechas* with inset showing a single flower spike.

2.2.3 a) Nectar

Nectar samples were taken approximately every two hours throughout the day, from 07:50 until 17:55. For each nectar sample, 20 spikes of *L. stoechas* flowers were picked from centre areas and 20 from edge areas, a maximum of two spikes being taken from any one clump. Nectar samples were taken from one spike of each in turn, using micro capillaries (as in section 2.1.5b) so that any evaporation after picking would be equal. The flowers were also placed in the shade to reduce evaporation. All the flowers from one spike were used but if this did not give enough nectar for a concentration reading then more than one spike was used. Nectar volume and concentration were recorded, together with the numbers of flowers and spikes needed to get these readings.

2.2.3 b) Visitors

Between the nectar sampling times, recordings of visitation were made, from 09:30 and 17:20 when most visitors were flying. Three "pairs" of *L. stoechas* clumps were chosen each day, one being "edge" and one being "centre". The two plants in a pair always had similar numbers of spikes. About once every hour and a half, all three pairs of clumps were watched. Each clump was observed for 10 minutes, alternating between centre and edge clumps. For each visitor arriving at a clump, the type of visitor was recorded as

- Coleoptera: Pollen feeding beetle (mostly chafers), Other beetle
- Diptera: Bombylid, Bibilionid, Other fly
- Hymenoptera: *Apis, Nomada, Anthophora, Melecta*, *Chalicodoma, Bombus*, Medium bee, (e.g. *Eucera/Synhalonia/Osmia spp.*), Tiny bee (e.g. *Ceratina sp.*)
- Lepidoptera: Lycaenid

The duration of each visit to a clump was also recorded. It was not possible to record the number of individual flowers or spikes each visitor went to, since that way only one visitor could be watched at a time.

Some visits were made by a species of bibionid fly. However these always visited the "flag" on top of the spike rather than the flowers themselves. Although they would probe the flag, as if it were a flower, they did not appear to succeed in collecting either nectar or pollen. These flies were therefore excluded from the analysis.

2.2.3. c) Plant size and density and flower number

One tape was laid out in a random direction across a very "patchy" area of scrub, and one across an area with very few open patches. Every time a clump of *L. stoechas* flowers was reached, the distance from the previous clump was recorded to give an idea of the density of clumps. This continued until 30 clumps had been counted. Each plant was recorded as "edge" or "centre" using the definitions given previously. The number of plants in the clump and the number of spikes on each plant were counted, for 30 "edge" plants and 30 "centre" plants. For each clump, 30 spikes were removed and the number of flowers on each was counted to give the mean number of flowers per spike for that clump. The height of the tallest plant in the clump was measured as was the diameter at the widest point and perpendicular to it. These three measurements were multiplied together to give an estimation of overall clump volume.

2.2.3 d) Seed-set

After the plants had gone to seed, 50 spikes were collected at random from edge plants and 50 from centre plants (a maximum of two from any one clump). Five pods were taken from each spike and the number of seeds in each pod was counted. Mean seed-set per pod was calculated for each area.

2.2.4 *Cistus creticus* study

Two sites were chosen for this study. The first site, "Vatera hill" (GPS lat. & long.: 26°11.4', 39°01.9), was 100m above sea level, in an area of wasteland consisting of *C. creticus* scrub with rough grass patches in between. The second site, "Olive Grove" (GPS lat. & long.: 26°10.4', 39°01.5) was close to sea level. Again most of this area was *C. creticus* scrub and had some edges bordering open patches of

grassland and others bordering newly ploughed land under olive trees. Visitor observations and nectar samples were made on four days as close together as possible in each site.

2.2.4 a) Nectar

Nectar was sampled every two hours between 09:00 and 15:00. Before this the flowers were not properly open and after 15:00 they shrivelled and the petals dropped off. At each sampling time, 20 flowers were picked from the centres of patches and 20 from the edges. Nectar volume and concentration were recorded for each one as before. The flowers were picked at random by choosing a direction, walking 2 paces and picking the nearest flower on the right each time.

2.2.4 b) Visitors

At the start of each day, three pairs of flower patches were chosen where around 20 flowers could be watched simultaneously. Individual bushes were not used since in areas of continuous *C. creticus* scrub individual bushes could not easily be separated. Each pair included one group of flowers in thick scrub ('centre') and one on an 'edge' with roughly equal numbers of flowers. At 09:30, 11:30 and 13:30 each patch was observed for 10 minutes, alternating between centre and edge patches. The number and type of visitors coming into the patch was recorded and also the length of time each visitor stayed in the patch. Visitors were recorded as:

- Coleoptera: Pollen feeding beetle (mostly chafers), Longhorn beetle, Weevil
- Diptera: Syrphid, Conopid, Other fly
- Hymenoptera: *Apis, Nomada, Bombus, Halictid*, Medium bee, (*Eucera/Synhalonia/Osmia*), Tiny bee (e.g *Ceratina sp.*), Wasp

- Lepidoptera: Satyridae (Browns), Hesperiidae (Skippers), *Vanessa cardui* (Painted lady).

Whether the visitor appeared to be a nectar feeder or solely eating pollen was also noted. This was generally obvious, since pollen feeders tended to land on one flower and remain there for several minutes, whereas nectar feeders made short visits to several flowers.

2.2.4 c) Flower size and density

Two 1m wide and 186m long transects were laid down, one through the middle of the *C. creticus* scrub area and another following the edges of the *C. creticus* patches in each site. A continuous line of $1m^2$ quadrats was laid along the left hand side of each transect and the number of flowers in each $1m^2$ area was counted. Size measurements were taken from 60 to 70 flowers in each area, using callipers (Mituotoyo 500-321). Flower diameter from the tip of one petal to the tip of the opposite petal was measured, and also 'centre diameter' which was the diameter of the anther surfaces as a whole, (see Figure 2.5).

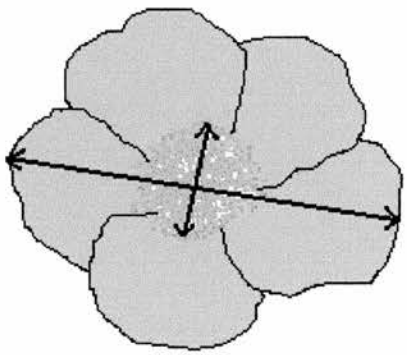


Figure 2.5. A *Cistus creticus* flower. Arrows show measurements taken.

2.2.4 d) Pollen

Thirty flowers were picked at random as for nectar sampling. The anthers from each flower were cut off and placed in a vial of 70% alcohol to be taken back to the UK. Each sample was made up to 3ml and sonicated for 10 minutes to remove all available pollen from the anthers and to separate clumps. The jar was shaken and immediately two 10µl sub-samples were placed on a slide. The total number of pollen grains in each sub-sample was counted and the mean number of grains calculated for each flower.

Due to the inaccuracy in previous measurements of pollen grains under a coverslip (Section 2.1.5 f), pollen grains in this study were measured without a coverslip. If this was done whilst they were still suspended in alcohol they would move around. In order to prevent this, the alcohol was allowed to evaporate. However there was some shrinkage of pollen grains as they dried. After 24 hours at room temperature no further shrinkage was seen, therefore for each sample, a 30 µl sample was placed on a slide and left to dry at room temperature for 24 hours. Thirty grains from each sub-sample were measured using an eyepiece graticle at x 200 magnification, and the mean diameter calculated.

2.3 Goat grazing and floral diversity.

Nine transects were surveyed on three days each, all in an area burnt in 1977 (24 years ago). These sites were at 500m intervals along the East side of the road between Achlederi (Grid Ref: 39°09.8', 26°16.40) and Agh. Nikolaos (39°10.90, 26°17.50). All were less than 100m above sea level. Initially four surveys were planned. However one made at the start of the season included only 7 sites, two of which later turned out to have been burnt more recently. These were therefore swapped for

different sites and an extra 2 were also included to give as much variation in grazing levels as possible. Thus only 3 surveys are used in the full analysis, though extra data are available for two of the sites.

The aims of this study were (a) to find out whether the effects of goat grazing on floral diversity and abundance were similar to the effects of cattle grazing observed in Israel and (b) to investigate a variety of grazing levels, in a large number of sites of one age, to see whether the relationship between flower diversity and abundance and grazing was unimodal or whether goat grazing simply had negative effects on floral diversity and abundance.

Vegetation heights were measured only on the first survey day and floral diversity and abundance and grazing levels were measured throughout the season. All these parameters were measured along a 60m transect in each site, which was split into 3 20m sections. The transects were perpendicular to the road so all were slightly higher at one end than the other. The same transect was repeated on each survey day. Vegetation height was measured at points every 0.5 m along each transect. Floral diversity was measured as for the biodiversity surveys (Section 2.1.4) and species lists are given in appendix 5. Floral abundance was measured as total flower area, calculated from an estimated flower diameter for each species. Since sheep and goat dung pellets are so small it was not possible to count them as was done for cattle. Dung levels were therefore recorded by laying out a 50m tape and recording presence or absence of dung in every 0.5 m^2 on either side (200 quadrats in total).

2.4 Exclosure Experiments

2.4.1 Exclosure in Israel.

This study took place in a field adjoining the Mitla site, described in Section 2.1.1. The area used was cleared for sheep grazing 25 years ago and has been grazed by cattle for the last 10 years. This site was chosen since it was known to be heavily used by cattle. On 20 March 2000, an exclosure of 12m x 6m was built, using metal posts with 4 strings of barbed wire around them. An area as similar as possible was marked outside the exclosure. Strips 10m x 0.5m were selected within these areas, and a different pair of strips were surveyed every 7-10 days until June.

The total number of each species of flower in each strip was counted and the average diameter of a flower estimated so that total flower area could be calculated for each species. The vegetation height to the nearest 5cm was measured every 0.5 m along one side of the strip. At the end of the season 40 measures of soil hardness were recorded using a penetrometer (Section 2.1.7), both inside and outside the exclosure.

Further exclosures were set up at the end of the season in 2000 at Mit Shed and Hod. Maps were drawn of vegetation cover within the exclosures and diameters of any shrubs or bushes measured. All three exclosures were to be surveyed throughout the spring in 2001. However it was not possible to return to these sites in 2001 due to the escalating political situation in Israel.

2.4.2 Exclosure in Lesvos

On 24 March 2001, 2 exclosures (12m X 10m) were set up. These exclosures were similar to those used in Israel but sturdier. Sheep netting was used for the main part

of the fence, and a length of barbed wire added along the top. One exclosure was placed in a mature *Pinus brutia* forest and one in an area burnt 2 years previously. Both areas were grazed by sheep and goats. Grazing levels were estimated in both areas as in section 2.3, but using 200 quadrats ($0.5m^2$) rather than 100. 47 % of all quadrats in the burnt area contained dung and 21.5 % of all quadrats in the mature area did.

Plots of the same size as the exclosures, and as similar as possible with regards to flora and shade, were marked outside the exclosures. In each plot, 4 strips (9m × 0.5m) were marked out with paths between them, so that the study strips were never walked on. These strips were surveyed 4 times between the 26 March and 18 May for flower abundance and diversity, vegetation height, soil hardness and nectar and pollen. Every flower in each strip was counted and identified, and flower diameter was estimated for each species, so that the total flower cover for each species could be calculated. Nectar and pollen samples were taken from ten flowers of each species (or as many as there were), from the gaps between the survey strips. However all the flowers were often from just one plant on one day, or else there were very few of any one species inside the exclosure. The sample number would have been very low, so these samples were not analysed.

Soil hardness was measured using a penetrometer as described in section 2.1.7. However actual values were recorded (rather than assigning values to categories as was previously done), 0 being softest and > 4.5 Kg m^{-2} being hardest. This way mean soil hardness could easily be compared between areas. Vegetation height was measured to the nearest 5cm, every 0.5m along one side of the strip. Nitrogen,

phosphorous and pH were measured at the start and end of the study as described above (Section 2.1.7).

2.5 Diversity Measurements and Statistical Methods

2.5.1 Measures of diversity

For both flowers and bees, species richness was used rather than any other measure of diversity since it is the simplest and most widely used diversity index in the literature and therefore our findings would be readily comparable with other published work. Although α diversity is generally considered the most robust measure of diversity (Magurran 1988), species richness and α diversity of bees in all sites in 1999 were found to be very highly correlated (R^2=98.2%, n=21, P=0.001), so that either measure would give the same conclusions. This is probably due to the fact that there were a large number of rare species (many singletons). Also, the relative abundances of species were likely to be inaccurate since some were more easily caught than others, meaning that it was safer simply to use species number.

It must be noted that only the bees caught or identified on the wing could be included in measures of species richness. The sample of species caught was only part of the actual number of species in a site, and therefore species richness tended to increase as more bees were caught. This means that although sites where bees are most abundant are likely have most species, measured species richness is also partly related to sample size.

2.5.2 Statistical Tests

All data sets were tested for normality using the Anderson-Darling normality test.

Where two independent sets of data were compared, t-tests were employed to compare means, unless data did not have a normal distribution, in which case medians were compared using Mann-Whitney *U* tests. Paired samples were compared using matched pairs t-tests if data were normally distributed and Wilcoxon's Signed Ranks tests when not.

Two-way Analysis of Variance was used to compare the abundances of three different soil hardness categories, inside and outside exclosures. It was also used in Chapter 5 to compare various measurements of flowers at edges and centres of vegetation patches in two different field sites.

To determine whether the relationship between bee species richness and flower species richness was the same across two years, analysis of covariance was used, rather than ANOVA, since one of the independent variables (flower species richness) was continuous. Year was the model variable, flower species richness was the covariate and a term was included for interactions between the effects of year and flower species richness. When an interaction proved not to be significant, this term was removed and the test was repeated to find out whether the other variable had significant effects. This test was also used to compare other relationships across years.

When testing for a linear relationship between two continuous variables, linear regression was used, providing that residuals were normally distributed and variables could clearly be assigned as cause and effect. If the residuals were not normal, then a Spearman's rank order correlation was used. If a curvilinear relationship was expected, then a polynomial regression was used as long as the residuals were normal. In some cases, exponential curves or rectangular hyperbolas were also fitted to the data using "Graph Pad, Prism". In one case the best fitting line was a rectangular hyperbola and the significance of this fit was tested using "Statistica".

Where there were several possible lines to fit a set of data, F-Tests were performed (using Graph Pad, Prism), to compare fits and show whether one line was a significantly better fit than any other. If the Degrees of freedom were equal for both lines, an F-Test was not necessary and the line with the highest R^2 was chosen. The same applied if the two lines had very similar R^2, in which case the line with the highest Degrees of Freedom was chosen.

Where several variables were inter-correlated and there were several possible mechanisms (or "routes") for a relationship, path analysis was employed (with EQS for Windows). This showed which variables were most closely related, allowing both direct and indirect causal relationships to be revealed, unlike other methods, which would only test direct relationships. However the results from these models should be regarded with caution since it was not possible to include every single potential relationship in a path diagram. As indices of the goodness of fit of the observed data to the whole path model, the Maximum Likelihood Chi Squared (χ^2), the Comparitive Fit Index (CFI) and the Root Mean Square Error of Approximation (RMSEA) are

given. For a good fit the χ^2 value should be low and P should be non-significant (0.05). If the P value is low (<0.05), then the observed data is not consistent with the causal process shown by the path diagram (Shipley 2000). RMSEA should also be low (<0.1) if the model is a good fit and CFI should be close to 1 (> 0.90, Arbuckle & Wothke 1999). Where the fit was not good (if P was < 0.05) alternative models were tested and the one with the lowest χ^2 value was presented, as long as the P-value was 0.05.

Since several variables had previously been shown to have curved relationships with dung levels (Chapter 4), the log of dung was used in path analysis to account for this. Where data were not normal, the logs or the square roots of the data were used. As well as measures of goodness of fit, path coefficients (partial regression coefficients) are given on the path diagrams in some cases. These values are given both as standardised and not standardised values. Standardised values are obtained by centring the variables (subtracting the mean value of each variable from each observation) so that they all have a mean of zero. In this case the units of the path coefficients are standard deviations from the mean. For values that are not standardised, the path coefficient measures the number of unit changes in "y" with a one unit change in "x" (Shipley 2000). These path coefficients are then tested using a z-test, to see whether they are significantly different from zero and significant values are shown with asterisks on the path diagrams.

A Best-Subsets Regression was used (Section 3.3.4) to determine whether species richness or abundance of flowers had the strongest effect on the bee communities, and whether bees were more limited by the floral resources available in the present or

previous year. Those variables shown to be most important by the Best-Subsets regression were then run through multiple regression tests to obtain P values.

When a single set of data was repeatedly tested against different variables, Sequential Bonferroni adjustments were made according to Rice (1988) in order to reduce the likelihood of obtaining a significant result by chance. Those variables included in Bonferroni adjustments are summarised in tables at the end of each section.

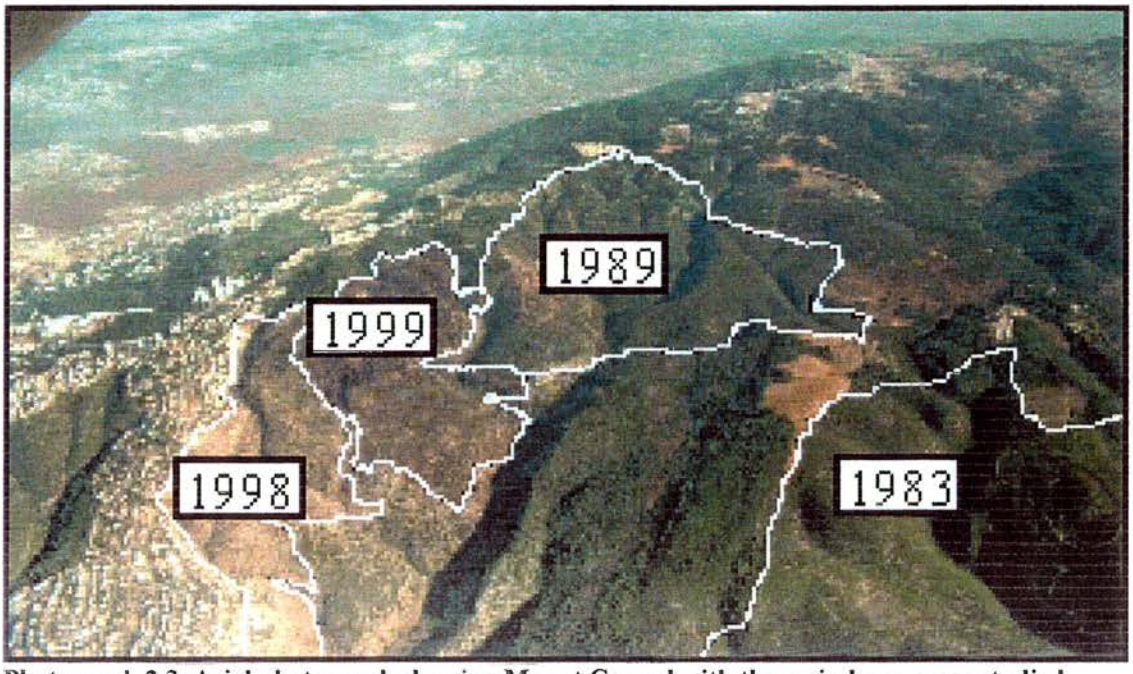
2.5.3 Abbreviations

Throughout all the following chapters, abbreviations are used to describe the statistical tests used. These are given in Table 2.2.

Test	Initials
Linear Regression	LR
Polynomial Regression	PR
F-Test	FTEST
Spearman's Rank Order Correlation	SROC
2 sample t-test	T-test
Mann-Whitney *U* test	MWU
Paired t-test	Paired T
Wilcoxon's Signed Ranks test	WSR
Analysis of Variance	ANOVA
Analysis of Covariance	ANCOVA
Chi squared	χ^2
Sequential Bonferroni Adjustment	SBA

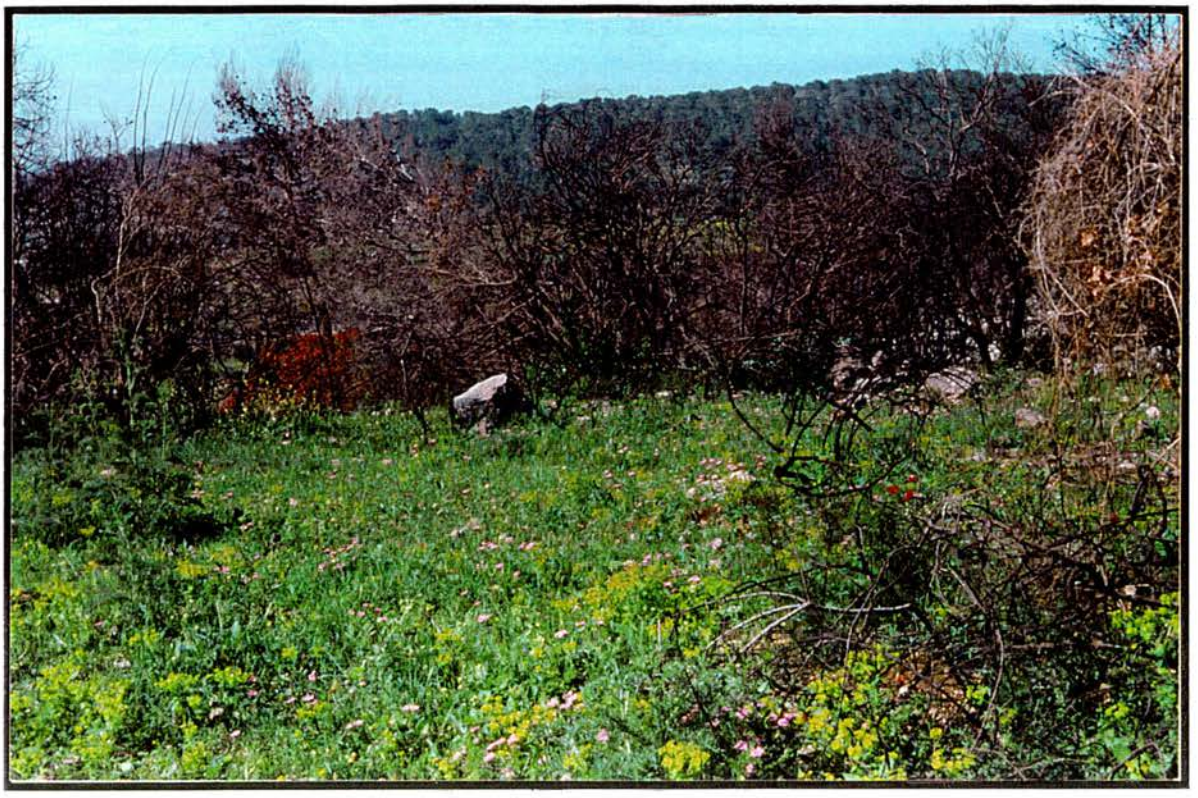
Table 2. 2 Abbreviations for statistical tests.

2.6 Habitat photographs



Photograph 2.3 Arial photograph showing Mount Carmel with the main burn areas studied. The 1998 burn shown is Den 98 and Hod 98 is hidden behind the mountain. Den NB was in the area which then burnt in 1999. The other mature sites were close to the 1983 burn and to Hod 98 and are not shown in this picture.

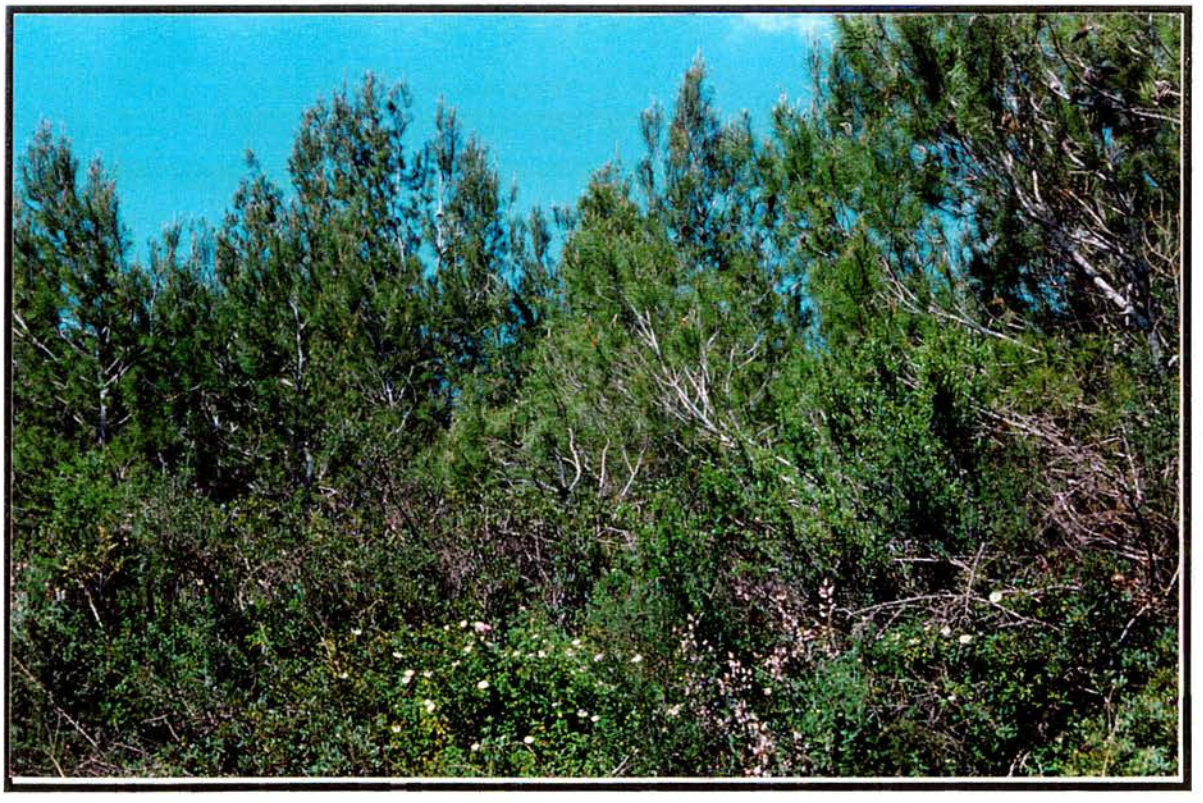
Photograph 2.4 Den 98, 4 months after fire.



Photograph 2. 5 Hod 98, 6 months after fire.

Photograph 2. 6 Haibar Nature Reserve, 10 years after fire.

Photograph 2.7 Mitla, 16 years after fire.



Photograph 2.8, Etz74, 25 years after fire.

Photograph 2. 9, EtzNB, mature forest, at least 50 years since fire.

3 The Effects of flowers and floral rewards on the diversity and abundance of bees

3.1 Introduction

Bees feed almost exclusively on nectar and pollen, therefore it is probably the availability and quality of flowering plants and their rewards that are the main factors limiting bee abundance and diversity. However bees may also be limited by other factors, such as the availability of nesting sites and materials, or the abundance of predators.

It seems likely that the overall abundance of bees will depend on the overall abundance of food sources (Faegri & van der Pijl 1979; Proctor *et al.* 1996). It is probably the total amount of energy available from floral rewards which is the limiting factor for bees, as found for pollen in Mediterranean habitats (Petanidou and Vokou 1990) but other nutrients such as water or proteins may also be important (e.g. Baker & Baker 1975, 1983; Willmer 1986). However most of the resources a bee gathers are to provision offspring which will emerge the following year, therefore the population of bees present in one year may be more directly limited by the resources that were available in the previous year. This was suggested by Tepedino and Stanton (1981) following work in high altitude shortgrass prairie in Wyoming, USA. They found no significant positive correlations between the abundance of a flower species and the number of bees visiting it within the same year, but this was believed to be due to due to variation in floral resources across years.

The diversity of bees is likely to be dependent on the diversity of food sources, rather than on their overall abundance. MacArthur (1972) considered that species diversity is a function of the diversity of resources available in a community, the proportion of the resources used by each species (niche breadth), and the average part of each niche shared with other taxa (niche overlap). Flowers provide a variety of foraging niches, since nectar and pollen vary in the amounts of energy, amino acids and other nutrients they contain. The accessibility of these resources also varies, due to floral architecture and phenology (Faegri & van der Pile 1979; Pellmyr 2002). Certain flower species therefore provide rewards which may only be useable by certain bee species.

Assuming that the species richness of flowers is an indication of the diversity of rewards available, then bee diversity should be closely linked to floral diversity. The species richness and abundance of bees have been found to be positively related to the species richness and abundance of flowers in set aside fields in Germany (Gathmann *et al.* 1994; Steffan-Dewenter and Tscharntke 2001) and to floral biomass across 14 communities in central California (Moldenke 1975). Heithaus (1974) showed that as the number of flower visitor species in a community increased, in lowland areas of Costa Rica, the average niche breadth (the proportion of the total available flower species, used by each visitor species) decreased. However, these results were not supported in highland areas, where niche breadth and species number were lower than predicted by the abundance of flowers. This suggests that floral resources were not the only limiting factor but that other elements such as environmental severity were also important.

Although these studies have related the diversity and abundance of flowers and bees, few have looked at the actual rewards available. One study (Petanidou and Vokou 1990) found that in Greek phrygana, plant species with higher pollen energy contents had greater pollinator diversity. However they also found that pollen from wind pollinated plants had higher energy levels than that from insect pollinated ones. When wind pollinated plants were excluded from the analysis, the relationship between pollen energy and pollinator diversity did not hold true, so it may simply have reflected the higher energy levels in pollen from insect-pollinated flowers.

In phryganic ecosystems, pollen rather than nectar seems to be the main floral reward. In a phryganic community in southern Spain, only 33% of 122 plant species were considered nectariferous (Herrera 1985), and in East Mediterranean garrigue, it was found that only 7.5% of 133 insect pollinated plants produced >0.5µl of nectar per flower (Petanidou & Vokou 1990). This is probably an adaptation of both flora and fauna to drought, since dilute nectar would be costly to produce when water is in short supply. Nectar which is over a certain viscosity cannot be used by many pollinators (Baker & Baker 1975; Corbet *et al.* 1979; Kingsolver & Daniel 1983; Petanidou & Ellis 1993), although some insects can extract this nectar by adding watery saliva first (Baker & Baker 1975; Dafni 1992). It could therefore be argued that bees in these areas would be dependent on pollen rather than nectar as an energy source. However pollen is slow to digest, so adult bees still need a supply of nectar to cope with their immediate energy needs (Simpson and Neff 1983). As well as being an important source of easily available energy, nectar may also be important as a source of water in dry habitats (Willmer 1986, 1988), hence even if pollen is the main reward used nectar may still be limiting to bee communities.

Those studies that have investigated the actual rewards available to bees have focused on rewards produced by individual plant species within a habitat, and the diversity and abundance of pollinators visiting each plant species. However none have looked at reward production on the scale of a whole habitat as is attempted here. Furthermore, although it has been suggested that pollen, rather than nectar, is the main reward in Mediterranean habitats, their relative importance to visitors have not been specifically tested.

In this chapter I investigate whether floral rewards are indeed the main limiting factors to bee communities in a variety of Mediterranean habitats; and if so, whether it is the diversity or the overall abundance of rewards, which is most important. I also investigate whether bees are generally most dependent on nectar or pollen, and I assess the relative importance of herb and shrub flowers, since this is relevant when looking at disturbance by grazing animals, as described in Chapter 4.

3.2 Comparing bees across years

During the year 2000 field season, fewer bees were caught or identified than in 1999. There was a mean decrease of 27.4 (± 10.7) % in number of bees caught or named per plot for the 7 main sites. However much of this was accounted for by the difference between DenNB which burnt down and NewNB which replaced it. If these sites are excluded there is a mean decrease of 18.3 (± 11.0) % in catch number (WSR: W=118.5, n=18, P=0.049) leading to a mean decrease in measured species richness of 32.1 (±7.7) % (WSR: W=163.0, n=18, P=0.001) as shown in Figure 3.1.

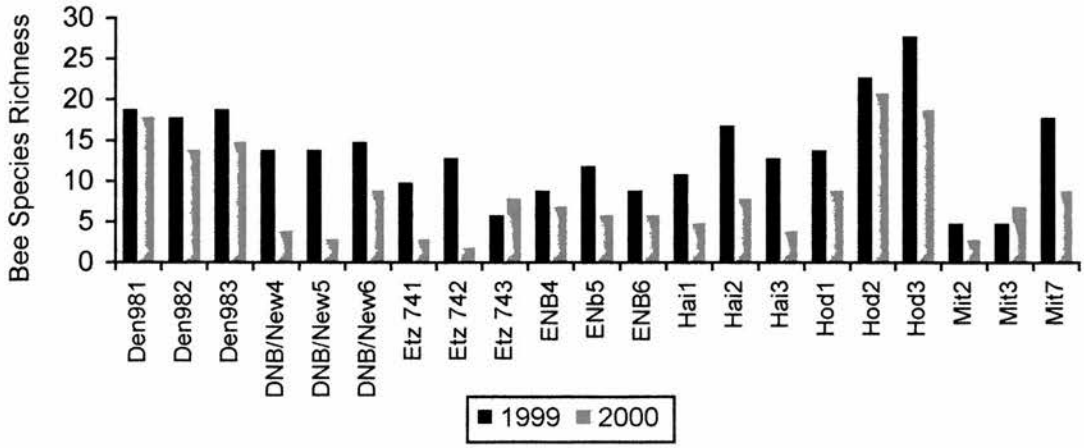


Figure 3.1 The change in measured bee species richness across years for the seven main sites surveyed over 5 rounds.

This was probably partly due to the fact that in 2000 most transects were done by one person for 20 minutes rather than 2 people for 10 minutes (See chapter 2). The difference in bee numbers across years may therefore be due to differences in the ability of catchers and in time spent in concentration on transects. Abundance of sighted bees did not change significantly across years at any of the 6 sites surveyed during both years (Paired T-test: T= -0.90, n=18, P=0.383) but NewNB had 63.5% fewer bees than DenNB, as shown in Figure 3.2.

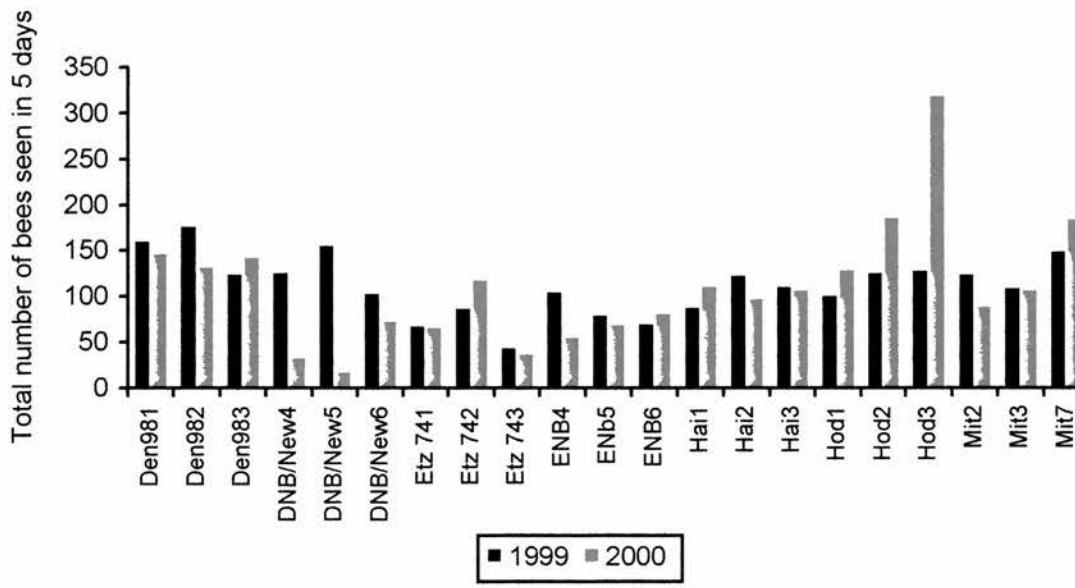


Figure 3.2 Bee abundance across years for the seven main sites surveyed over 5 rounds.

Since measured bee species richness for 2000 correlates well with that for 1999 (SROC: r_S=0.735, n=18, P<0.001), it is assumed that a reasonable sub-sample was caught on each occasion, which can be used to compare species richness across plots within one year. For much of the analysis of year 2000 data, only the last 3 rounds in the season are used, since the most highly grazed sites were only included for these surveys. Data for bee species richness in the last three rounds in 2000 also correlate well with those for 5 rounds in 1999 (Figure 3.3, SROC: r_S=0.811, n=18, P<0.001).

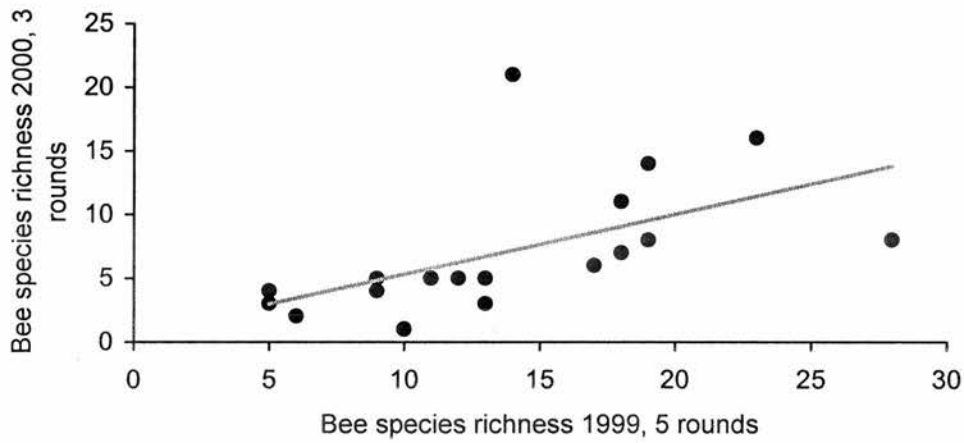


Figure 3.3 Relationship between measured bee species richness for 3 rounds in 2000 and 5 rounds in 1999, for the 6 sites surveyed in both years, with 3 replicate plots in each site.

3.2.1 Summary of section 3.2

- Fewer bees were caught in 2000 than in 1999, therefore measures of species richness were lower.
- Bee abundance did not change between the two years.
- The sub-sample of bees caught in 2000 was adequate for comparison of species richness across sites.

3.3 The relationship between diversity and abundance of bees and flowers.

Sequential Bonferonni tests mentioned in this section were done according to the 30 tests shown in the summary table at the end of section 3.3.

3.3.1 Bee Species Richness

Bee species richness did increase significantly with flower species richness in 1999 (SROC: r_S=0.680, n=21, P<0.001), in 2000 (SROC: r_S=0.699, n=30, P<0.001) and using all the available data combined (SROC: r_S=0.569, n=51, P<0.001) as in Figure 3.4. Bee species richness also showed a trend for increasing with flower abundance in 1999 (SROC: P=0.029, r_S =0.447, n=21, NS after Bonferonni adjustment), which was significant in 2000 (SROC: r_S=0.593, n=30, P=0.001); and using all available data combined (SROC: r_S=0.549, n=51, P<0.001) as in Figure 3.5.

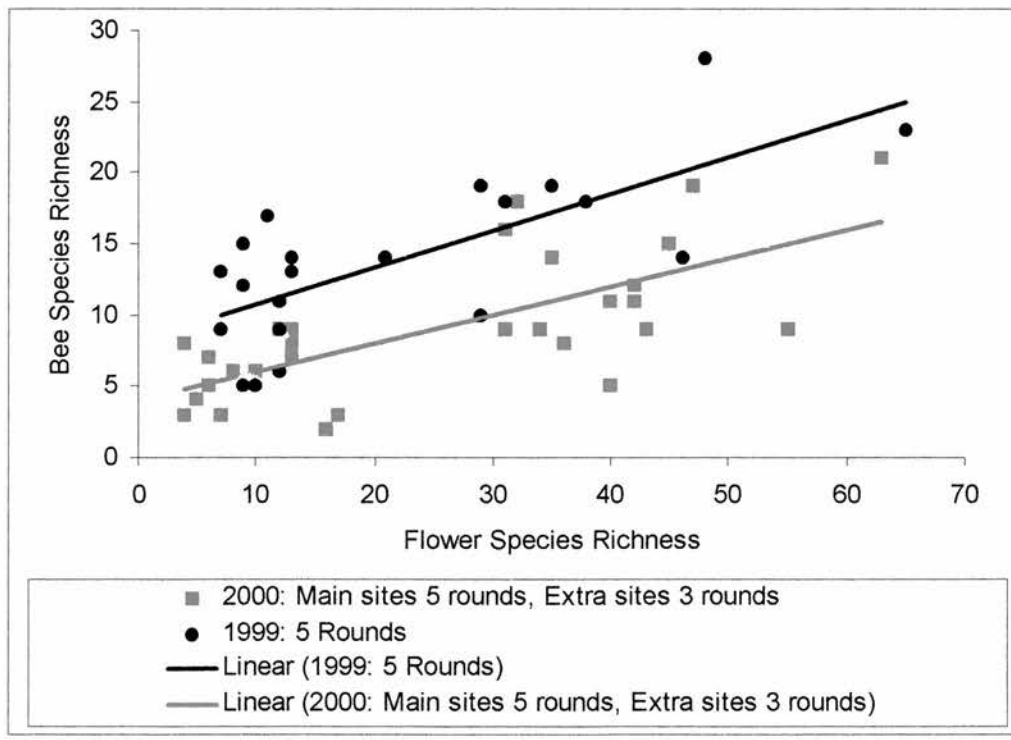


Figure 3.4: The relationship between bee species richness and flower species richness across 2 years using all the available data. N.B. There are 2 points for each plot in the 7 main sites and data from the extra sites are from 3 days surveys only.

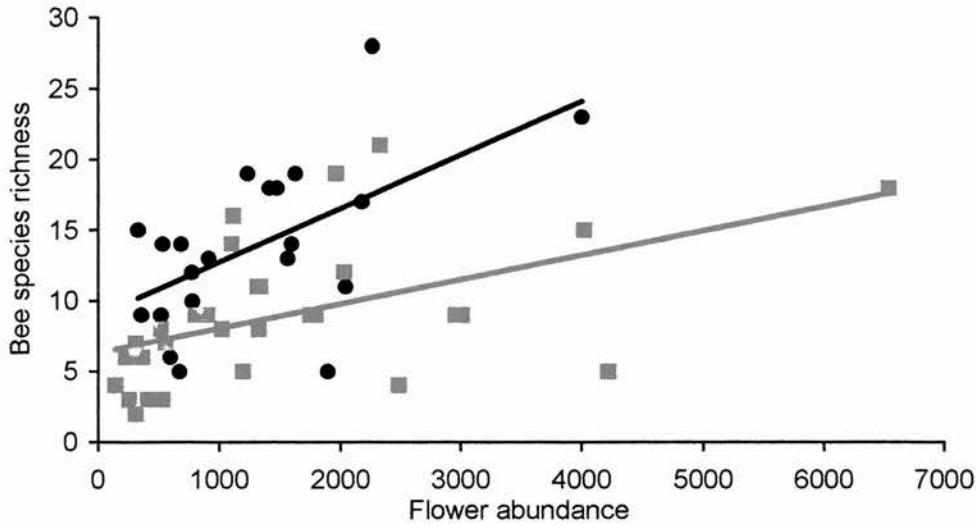


Figure 3.5 The relationship between bee species richness and flower abundance across 2 years using all the available data.

It can be seen from Figure 3.4 that the relationships between bee species richness and flower species richness were similar in 1999 and in 2000. An ANCOVA comparing the two years and using flower species richness as a covariate (Table 3.1 a), shows that there was no significant interaction between flower species richness and year, and therefore that the slopes of the two lines are not different (F=1.95, Adj MS=30.40, D.F=1,47, P=0.169). However, when the non-significant interaction term is removed (Table 3.1b), the effect of year is significant, showing that the intercepts of the two lines differ, so at any given level of flower species richness, bee species richness was significantly lower in 2000 than in 1999.

Source	DF	Adj MS	F	P
Log Flower species richness	1	637.05	40.84	<0.001
Year	1	0.71	0.05	0.832
Year*Log Flower species richness	1	30.4	1.95	**0.169**
Error	47	15.6		
Total	50			

Table 3.1 a) ANCOVA for the effects of year and flower species richness on bee species richness, including terms for the interaction between year and flower species richness.

Source	DF	Adj MS	F	P
Log Flower species richness	1	632.22	39.74	<0.001
Year	1	320.83	20.17	**<0.001**
Error	48	15.91		
Total	50			

Table 3.1b) ANCOVA for the effects of year and flower species richness on bee species richness.

This was similar when bee species richness was plotted against flower abundance as in Figure 3.5. The interaction between flower abundance and year was not significant (Table 3.3 a: F=0.85, Adj MS=17.18, D.F=1,47, P=0.362) showing that the relationship between flower abundance and bee species richness was the same in both years. Again, when the insignificant interaction term is removed (Table 3.2 b), year has a significant effect, showing that bee species richness was lower at any given level of flower abundance in 2000 than in 1999. The lower bee species richness in 2000 was probably due to differences between catchers, as described in section 3.1 but the fact that the pattern of these relationships does not change across years supports the idea that a good sub-sample was collected.

Source	DF	Adj MS	F	P
Log Flower abundance	1	395.51	19.5	<0.001
Year	1	5.5	0.27	0.605
Year*Log Flower abundance	1	17.18	0.85	**0.362**
Error	47			
Total	50			

Table 3.2 a) ANCOVA for the effects of year and flower abundance on bee species richness including terms for the interaction between year and flower abundance.

Source	DF	Adj MS	F	P
Log Flower abundance	1	425.28	21.03	<0.001
Year	1	286.69	14.18	**<0.001**
Error	48	20.22		
Total	50			

Table 3.2 b) ANCOVA for the effects of year and flower abundance on bee species richness.

3.3.2 Bee abundance

In 1999, bee abundance showed a trend for increasing with flower species richness (SROC: r_S=0.425, n=21, P=0.055) as shown in Figure 3.6. In 2000, bee abundance did increase with flower species richness (SROC: r_S=0.554, n=30, P=0.001) as it did with both years combined (SROC: r_S=0.547, n=51, P=0.001). Bee abundance also showed a trend for increasing with flower abundance in 1999 (r_S–0.330, n=21, P=0.137) as in Figure 3.7, though this was not significant. This trend was significant in 2000 (SROC: r_S=0.632, n=30, P<0.001) and with both years combined (SROC: r_S=0.494, n=51, P<0.001).

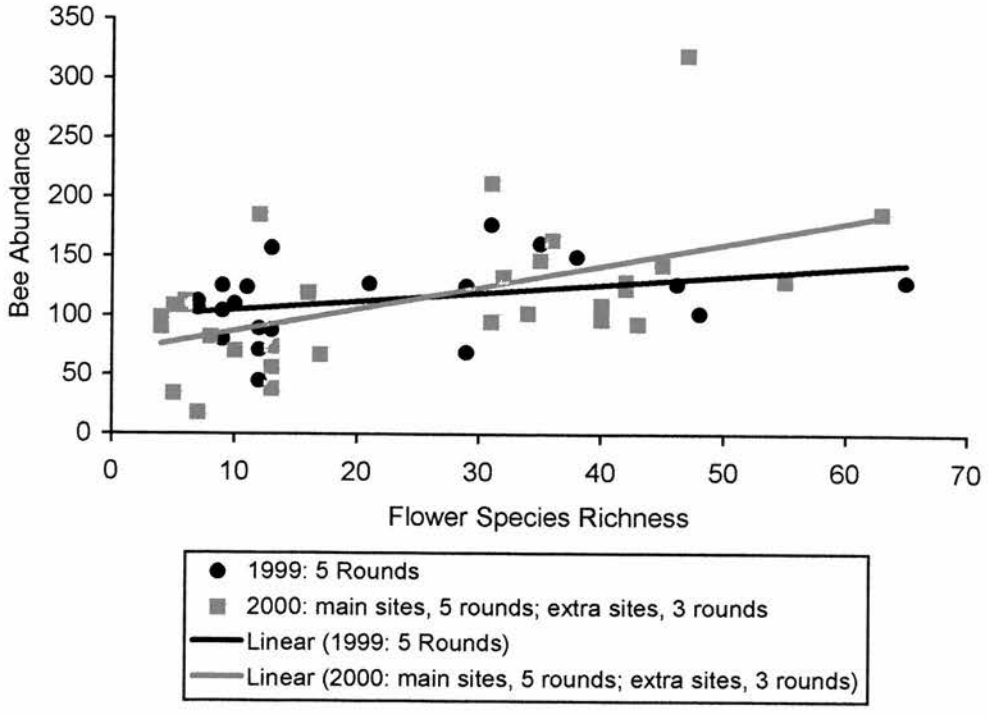


Figure 3.6 The relationship between bee abundance and flower species richness across 2 years using all the available data.

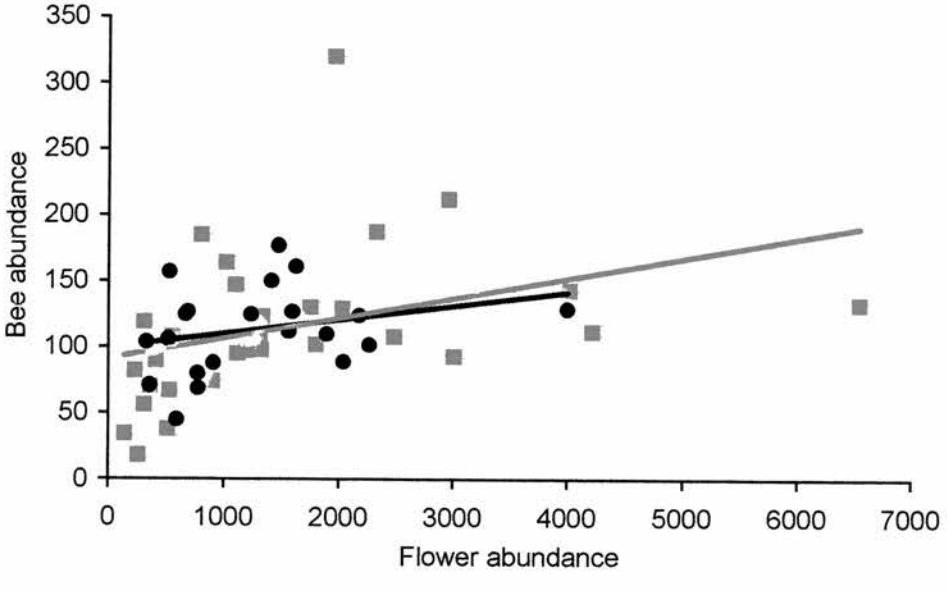


Figure 3.7: The relationship between bee abundance and flower abundance across 2 years using all the available data.

It seems from Figure 3.7 that bee abundance increased steeply initially and then began to level out at higher flower abundances. This suggests that flower abundance is only limiting up to a point, after which other variables become more important.

ANCOVA was used to look at the effects of year on bee abundance, with flower species richness, then flower abundance as covariates. This showed no significant interaction between flower species richness and year, (Table 3.4 a), F=0.83, Adj MS=1662, D.F=1,47, P=0.366) or between flower abundance and year (Table 3.5 a), F=0.91, Adj MS=1763, D.F=1,47, P=0.345). The relationships between bee abundance and flowers were therefore similar in both years. Removing the insignificant interaction terms showed no significant effects of year, therefore the number of bees was the same in both years, at any given level of flower species richness (Table 3.4b) or flower abundance (Table 3.5 b).

Source	DF	Adj MS	F	P
Log Flower species richness	1	18411	9.22	0.004
Year	1	1540	0.77	0.384
Year*Log Flower species richness	1	1662	0.83	**0.336**
Error	47	1997		
Total	50			

Table 3.4 a) ANCOVA for the effects of year and flower species richness on bee abundance with terms for interaction between year and flower species richness.

Source	DF	Adj MS	F	P
Log Flower species richness	1	27581	13.86	0.001
Year	1	1	0	**0.984**
Error	48	1990		
Total	50			

Table 3.4 b) ANCOVA for the effects of year and flower species richness on bee abundance.

Source	DF	Adj MS	F	P
Log Flower abundance	1	16666	8.61	0.005
Year	1	1675	0.87	0.357
Year*Log Flower abundance	1	1763	0.91	**0.345**
Error	47	1936		
Total	50			

Table 3.5 a) ANCOVA for the effects of year and flower abundance on bee abundance with terms for interaction between year and flower abundance.

Source	DF	Adj MS	F	P
Log Flower abundance	1	30362	15.72	<0.001
Year	1	63	0.03	**0.857**
Error	48	1932		
Total	50			

Table 3.5 b) ANCOVA for the effects of year and flower abundance on bee abundance.

3.3.3 Diversity related to abundance

Bee species richness also correlated positively with bee abundance in 1999 (SROC: r_S= 0.664, n=21, P<0.001), in 2000 (SROC: r_S=0.627, n=21, P<0.001) and with data from both years (SROC: r_S=0.540, n=51, P<0.001) as shown in Figure 3.8. Figure 3.9 shows that flower species richness tended to increase with flower abundance in 1999 (SROC: r_S=0.480, n=21, P=0.028), though this was not significant after SBA. This relationship was significant in 2000 (SROC: r_S=0.515, n=21, P=0.004) and with both years combined (SROC: r_S=0.508, n=21, P<0.001).

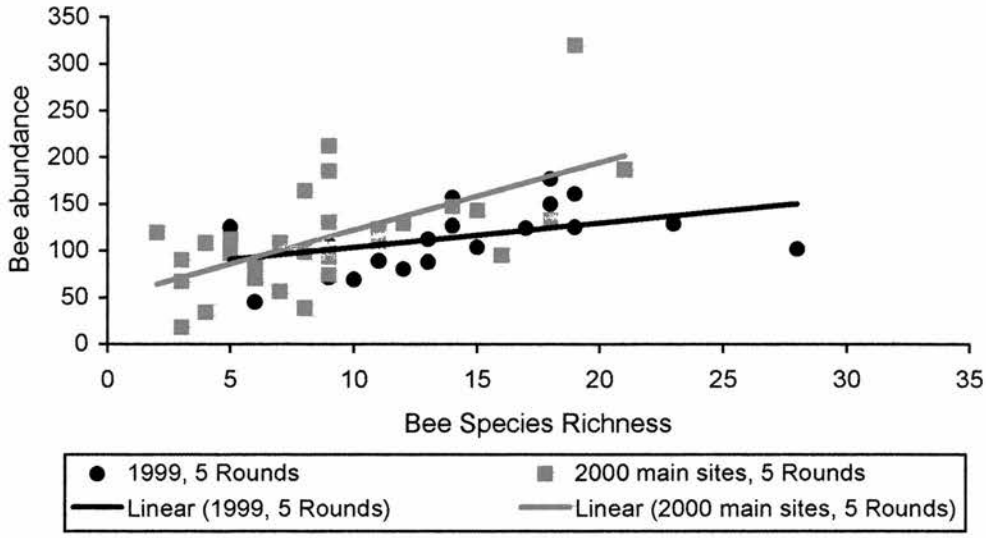


Figure 3.8 Bee abundance plotted against bee species richness for 1999 and 2000.

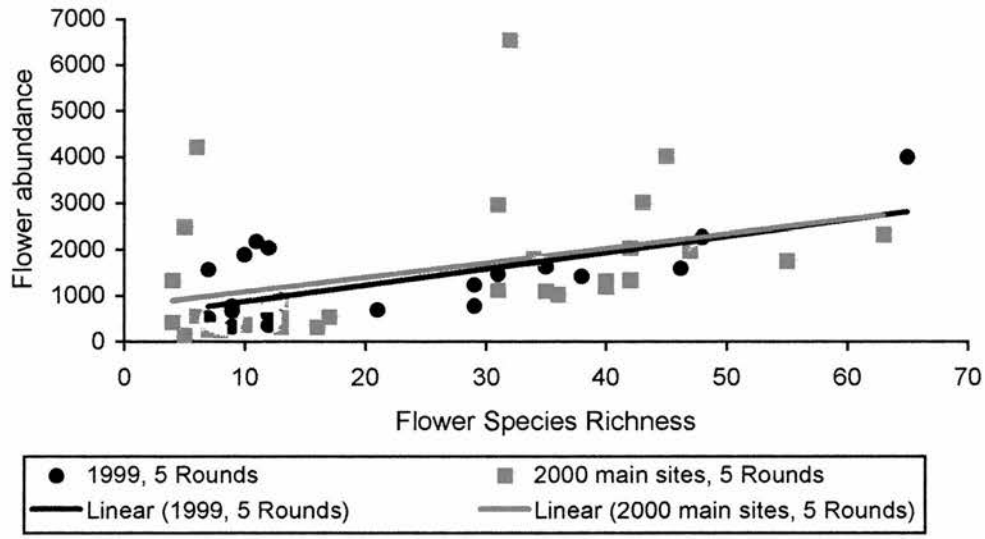


Figure 3.9 Flower abundance plotted against flower species richness for 1999 and 2000.

Thus bee and flower abundance are closely related to bee and flower species richness, but it is not possible to tell which the cause and which is the effect. Species richness may increase abundance if there is little overlap between niches. If there are more species in more separate niches, there will be less competition so it may be possible for a greater number of flowers or bees to survive in one place. However a greater abundance may also cause an increase in species richness due to its effect on sample

sizes. If a site had a higher abundance of bees or flowers, the sample size was larger and therefore there was more chance of detecting a higher number of species.

Path analysis (Figure 3.10) shows that Flower species richness had a direct positive effect on the number of bee species and on bee abundance, but also had indirect effects via increased flower abundance. Flower abundance also had both direct and indirect effects on both bee species richness and bee abundance. Since this model gave a low χ^2 value (0.000) and a high P-value (1.0), this shows that the model is not significantly different from the observed data.

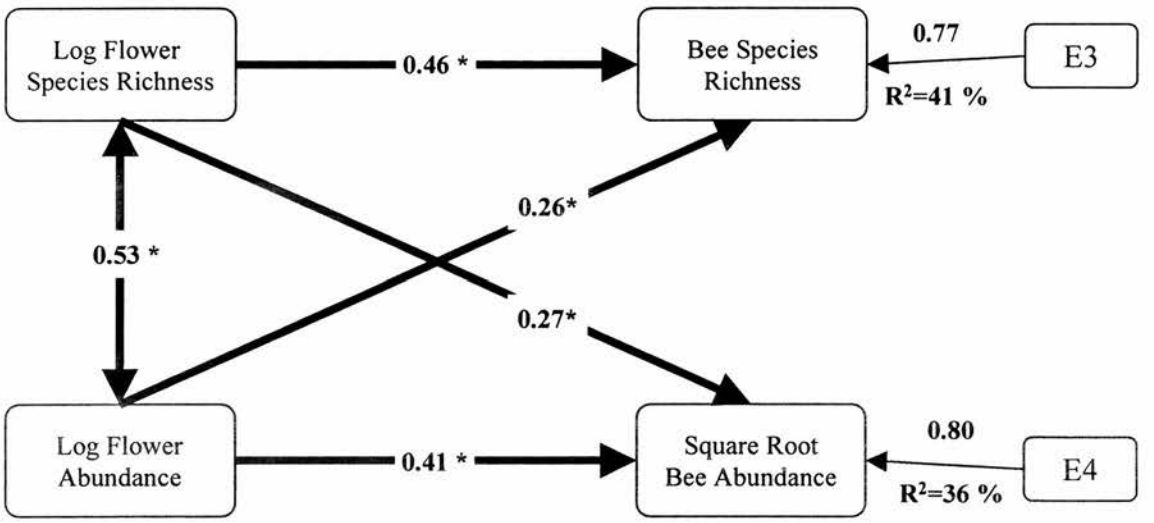


Figure 3.10 EQS Model Using all data from both years, relating log flower species richness and log flower abundance to bee species richness and square root bee abundance. χ^2=0.000, P=1.00, CFI=1.00, RMSEA=0.00. Lines in bold and numbers with * show significant relationships , numbers represent standardised partial regression coefficients. R^2 shows the amount of variation in one variable that is explained by the whole path diagram. E3 and E4 show variation caused by unidentified variables.

Overall 41% of the variation in Bee species richness and 36% of the variation in bee abundance are explained by this model. It seems that both abundance and species richness of flowers were important in determining bee species richness, but that flower abundance was the most important factor in determining bee abundance and

flower species richness was the most important in determining bee species richness. However this model is incomplete since there is no connection between bee abundance and bee species richness. A one directional arrow can be put in this place, but whichever direction it points in, it has a partial regression coefficient of 0.20 and is not significant, therefore makes no difference to the rest of the model. This model is also incomplete since it assumes that flower abundance and species richness are the only known variables affecting bees. A more detailed model will therefore be looked at in chapter 4.

3.3.4. Delayed effects of 1999 flowering on 2000 bees.

Using the 6 main sites surveyed in both years, bee species richness in 2000 was also positively related to flower species richness in the previous year (Figure 3.11 a) and bee abundance (Figure 3.11 b) in 2000 was positively related to both flower species richness and abundance in the previous year (1999) as shown in Table 3.6. This is not surprising, because although many bees will have moved into a site due to the rewards available in contemporary time, many bees (especially of those species which do not travel long distances), may have originated from nests within the area. These bees were therefore the product of rewards available on the site, in the previous year, which were collected and stored by females of the previous generation.

	1999 Flower species richness	1999 Flower abundance
2000 Bee abundance	**P<0.001** r_S=0.757 n=18	**P=0.002** r_S=0.686 n=18
2000 Bee species richness	**P=0.002** r_S=0.675 n=18	P=0.032 r_S=0.506 n=18

Table 3.3 Statistical values for Spearman's signed ranks correlations, relating bee abundance and species richness in 2000 to flower abundance and species richness in 1999 and 2000. Data are only from the 6 main sites which were surveyed for 5 rounds in both years. Figures in bold show those P values still significant after Bonferroni adjustment.

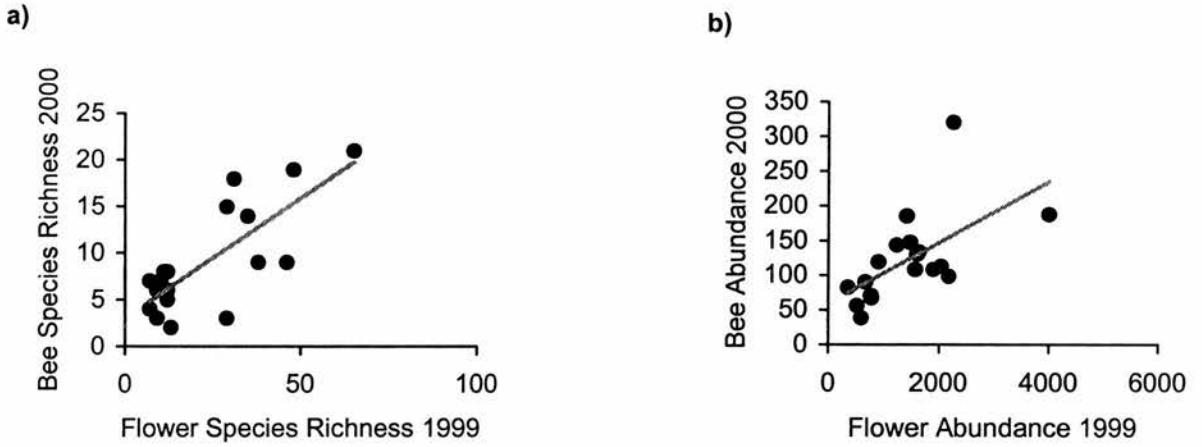


Figure 3.11 a) Bee species richness 2000 related to flower species richness 1999, b) Bee abundance 2000 related to flower abundance 1999 using the 6 sites surveyed in both years.

A best-subsets regression using the 6 sites surveyed in both years (Table 3.7), shows that both flower abundance and species richness in both 1999 and 2000, all play some part in explaining bee species richness in 2000 (R^2=56%, n=18, P=0.022). However, the most important variable is flower species richness in 2000, followed by flower species richness in 1999 and then flower abundance in 2000 which altogether explain 55.9 % of the variation in bee species richness. The variation in bee abundance in 2000 is explained mainly by flower abundance in the previous year (1999), but flower species richness in 1999 is also important as is flower species richness in 2000. These three variables together explain 64.1% of the variation in bee abundance (n=18, P=0.002).

	R^2	P(from multiple regression)	Variables included			
			Log flower species richness 1999	Log flower species richness 2000	Log flower abundance 1999	Flower abundance 2000
Explaining bee species richness in 2000	43.1	0.003		X		
	42.2	0.004	X			
	54.5	0.003		X		X
	53.3	0.003		X	X	
	55.9	0.008		X	X	X
	55.1	0.009	X	X		X
	56	0.022	X	X	X	X
Explaining bee abundance in 2000	51.2	0.001			X	
	45.7	0.002	X			
	63.8	<0.001	X		X	
	58.6	0.001		X	X	
	64.1	0.002	X	X	X	
	63.9	0.002	X		X	X
	64.1	0.007	X	X	X	X

Table 3.4 Best subsets regressions explaining bee communities in year 2000. N.B. P values come from multiple regression. Xs show those variables which were included in each part of the analysis. B.B. Log transformations were used where the data did not have a normal distribution otherwise.

Overall it seems that bee species richness is explained slightly better by the flowers in the present year whilst bee abundance is affected more by those in the previous year. This makes sense since the species richness of bees caught in one year will reflect the species richness of the flowers they are foraging on at that time and will include bees which have come from elsewhere, due to the flower species available. Total bee biomass on the other hand, will depend mainly on the total abundance of resources that were available in the previous season. Even if there was a low abundance of flowers in one year, there may still be a high abundance of bees which emerged in that site due to plentiful resources in the previous year. As suggested by the path analysis above, bee species richness is dependent mainly on flower species richness but flower abundance also plays a part. Bee abundance is mainly dependent on flower abundance and flower species number has an effect.

3.3.5 Shrub and herb flowers

Flower data from 2000 were split into herb flowers and shrub flowers. A herb was defined as any vascular plant that does not develop a woody stem (after Blamey and Grey-Wilson 1993) and a shrub was any plant which does develop a woody stem but was less than 3m tall when surveyed. Anything over 3m tall was counted as a tree. This means that flowering trees such as *Arbutus andrachne* were included as shrubs. Overall, shrubs made up 31 (±5.2)% of flower species and 42 (±7.0)% of flower cover.

Figure 3.12 shows that the bee communities were mainly dependant on the abundance of herb flowers rather than shrub flowers. Bee species richness and abundance increased with the abundance and species richness of herb flowers but were not affected by the abundance or species richness of shrub flowers (See Table 3.7 for statistics).

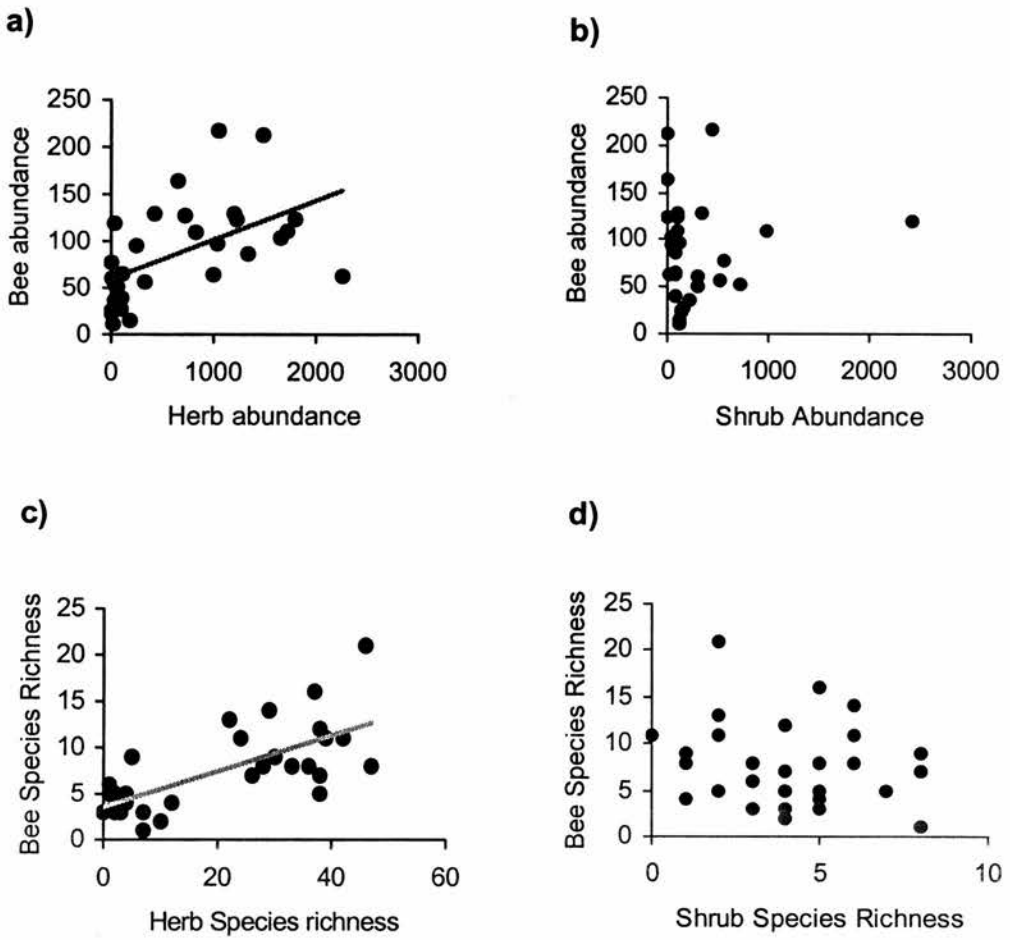


Figure 3.12 Bee abundance with: a) herb flower abundance, b) Shrub flower abundance. Bee species richness with: c) Herb flower species richness, d) Shrub flower species richness. All data is from 2000 only.

	2000 herb abundance	2000 herb species richness	2000 shrub abundance	2000 shrub species richness
2000 Bee abundance	**P<0.001** r_S= 0.640 n=30	**P<0.001** r_S= 0.636 N=30	P=0.257 r_S= -0.214 n=30	P=0.301 r_S= -0.195 n=30
2000 Bee species richness	**P<0.001** r_S= 0.639 n=30	**P<0.001** r_S= 0.658 N=30	P=0.472 r_S= -0.136 n=30	P=0.505 r_S= -0.192 n=30

Table 3.5 Statistical values for Spearman's rank order correlations, relating bee abundance and species richness in 2000 to abundance and species richness of herb and shrub flowers. Figures in bold show significant P values after SBA.

3.3.6 Summary of Section 3.3

	Flower abundance			Bee species richness			Bee abundance		
	1999	**2000**	**Both years**	**1999**	**2000**	**Both years**	**1999**	**2000**	**Both years**
Flower SR 1999	0.028			**<0.001**	**0.002**		0.055	**<0.001**	
Flower SR 2000		**0.004**			**<0.001**			**0.001**	
Flower SR Both			**<0.001**			**<0.001**			**0.001**
Flower Ab 1999				0.029	0.032		>0.05	**0.002**	
Flower Ab 2000					**0.001**			**<0.001**	
Flower Ab Both						**<0.001**			**<0.001**
Bee SR 1999							**<0.001**		
Bee SR 2000								**<0.001**	
Bee SR Both									**<0.001**
Herb Ab 2000					**<0.001**			**<0.001**	
Herb SR 2000					**<0.001**			**<0.001**	
Shrub ab 2000					>0.05			>0.05	
Shrub SR 2000					>0.05			>0.05	

Table 3.6 Summary of the relationships between flowers and bees. Figures show P values, NS =P-value >0.05. Those in Bold are still significant after SBA.

- Both flower abundance and species richness increase bee abundance and species richness.
- Herb flowers are more important to bee communities than shrub flowers are.
- Flower species richness in the present year is the main factor determining bee species richness.
- Flower abundance in the previous year is the main factor determining bee abundance.
- All these factors are important and all are interconnected, and there are also other factors affecting bees, which will be mentioned later in this Chapter and in Chapter 4.

3.4 The effects of floral rewards on the diversity and abundance of bees.

Sequential Bonferroni adjustments were made according to the 30 tests in the summary table at the end of this section (Table 3.10).

3.4.1 Nectar

Nectar energy from bagged and un-bagged quadrats were highly correlated (SROC: r_S =0.897, n=21, P<0.001), though bagged nectar values were on average 7.6 (±1.9) times higher than un-bagged values. Bagged values were therefore used in the analysis since it was easier to get accurate readings from flowers containing more nectar.

There was no significant relationship between bee abundance and energy from nectar in 1999 (LR: R^2 =24.8%, n=21, P=0.021, NS after SBA). Neither was there any relationship in 2000 (r_S=0.235, n=30, P=0.211), or with all the available data from both years combined (r_S=-0.820, n=51, P=0.889). See Figure 3.13.

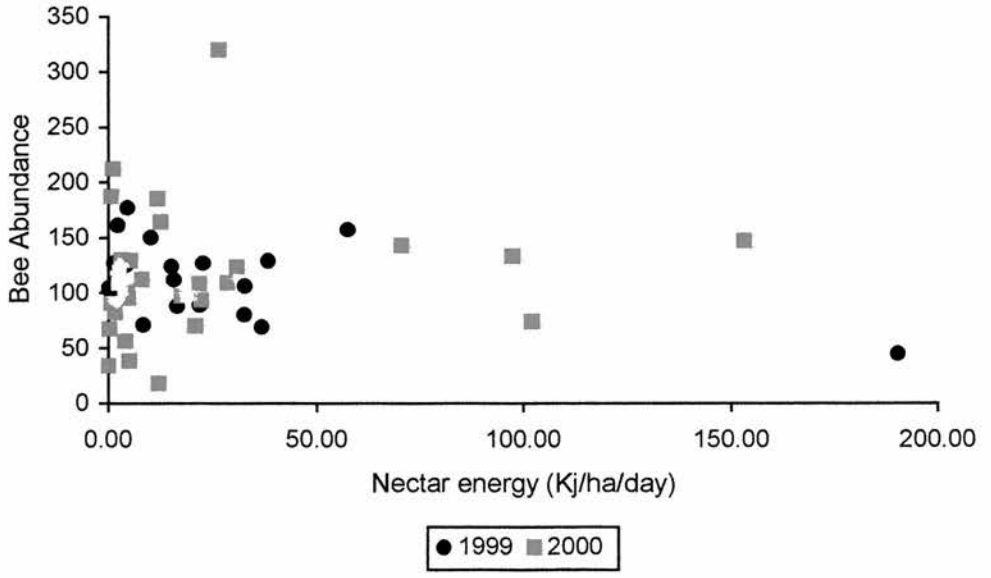


Figure 3.13 Bee abundance related to nectar energy.

Bee species richness was not affected by the amount of energy available from nectar in 1999 even when the outlier (Etz74 3) was removed (both P>0.05). In 2000 bee species richness showed a trend for increasing with the availability of energy from nectar as shown in Figure 3.14, but this was not significant after SBA (SROC: r_S=0.436, P=0.016, n=21). When both years were combined, this was still not significant (R^2=0.4%, n=51, P=0.668).

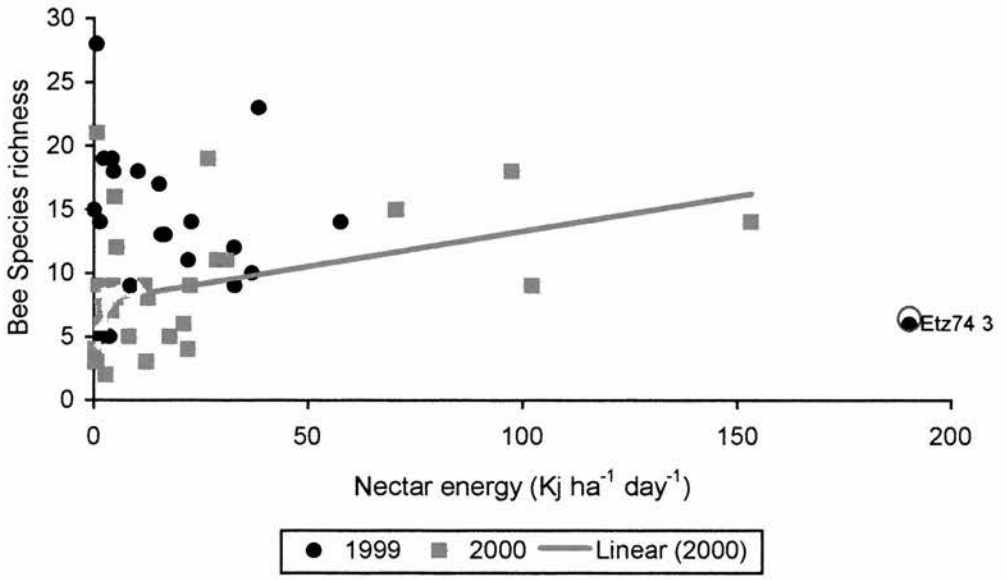


Figure 3.14 Bee species richness related to nectar energy. Main sites are surveyed over 5 rounds and Shed and bottom surveyed for three rounds only. Point circled in blue = outlier, Etz 74, referred to in text.

The volume of water available from nectar did not affect bee abundance or species richness in 1999, in 2000, or with both years combined (all P>0.05). Overall, bee abundance and diversity did not seem to be limited by nectar availability. However bee species richness **was** found to be related to the diversity of nectar niches by Potts et al, (Unpublished manuscript). In this analysis, nectar samples from each flower species were assigned to 9 different categories, according to their mean volumes and concentrations. These ranged from small volumes of highly concentrated nectar, to

large volumes of dilute nectar. The number of different nectar types present in a site was then used as an index of nectar niche diversity.

Since nectar sources were often very patchily distributed, it was thought that they may be used more by social bees which use large amounts of energy and are able to travel long distances and to recruit foragers to a patch of high rewarding flowers. This was tested for *Apis mellifera.* However *Apis* abundance and nectar energy were not significantly related (SROC: r_S=-0.073, n=30, P=0.700) in 2000.

3.4.2 Pollen

3.4.2.a) Pollen volume

Bee species richness was not related to the volume of pollen either in 1999 (SROC: r_S=0.266, n=21, P=0.243) or 2000 (SROC: r_S=0.266, n=30, P=0.168) separately or when both years were combined (SROC: r_S=0.304, n=51, P=0.030, NS after SBA) Figure 3.15.

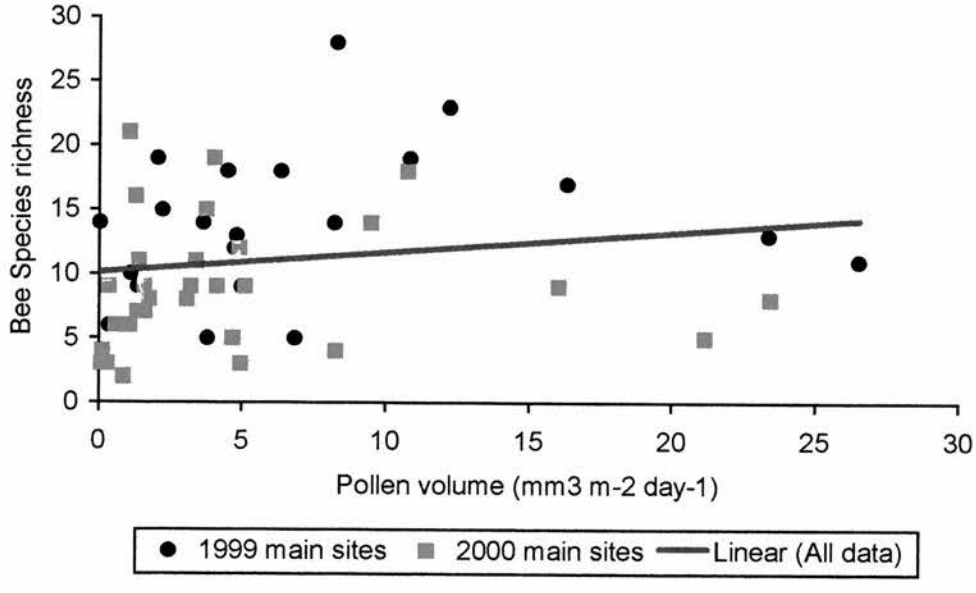


Figure 3.15 Bee species richness related to pollen volume. Main sites are surveyed over 5 rounds and Shed and bottom surveyed for three rounds only.

Bee abundance was not related to pollen volume in 1999 (SROC: r_S=0.201, n=21, P=0.383), in 2000 (SROC: r_S=0.393, n=30, P=0.032, NS after SBA) or when both years were combined (SROC: r_S=0.309, n=51, P=0.027 NS after SBA) as in Figure 3.16.

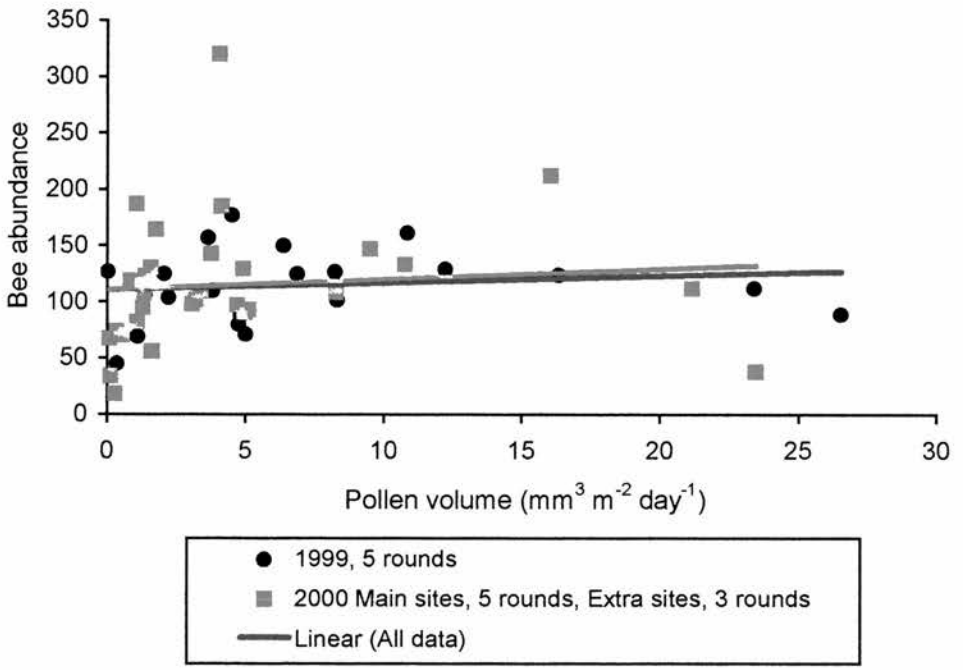


Figure 3.16 : The relationship between bee abundance and pollen volume across 2 years using all the available data.

3.4.2.b) Pollen grain number

Bee abundance was not correlated with pollen grain number in 1999 (SROC: r_S=0.254, n=30, P=0.266) but was positively correlated with pollen grain number in 2000 (SROC: r_S=0.580, n=30, P=0.001) and with both years combined (SROC: r_S=0.453, n=51, P=0.001) as in Figure 3.17.

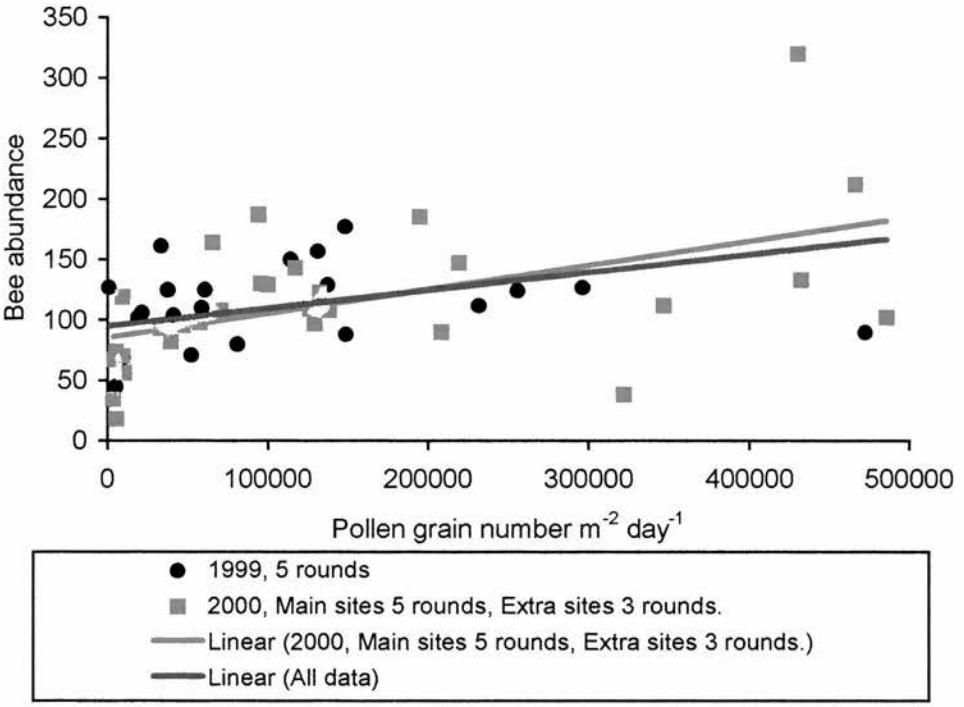


Figure 3.17: The relationship between bee abundance and grain number across 2 years using all the available data. N.B. There are 2 points for each plot in the 7 main sites and data from the three extra sites is from 3 days surveys only.

Bee species richness was also independent of grain number in 1999 (SROC: r_S=0.276, n=21, P=0.226). However there were positive trends in 2000 (SROC: r_S=0.401, P=0.028, n=30, NS after SBA) and with both years (SROC: r_S=0.306, n=51, P=0.029, NS after SBA) as shown in Figure 3.18.

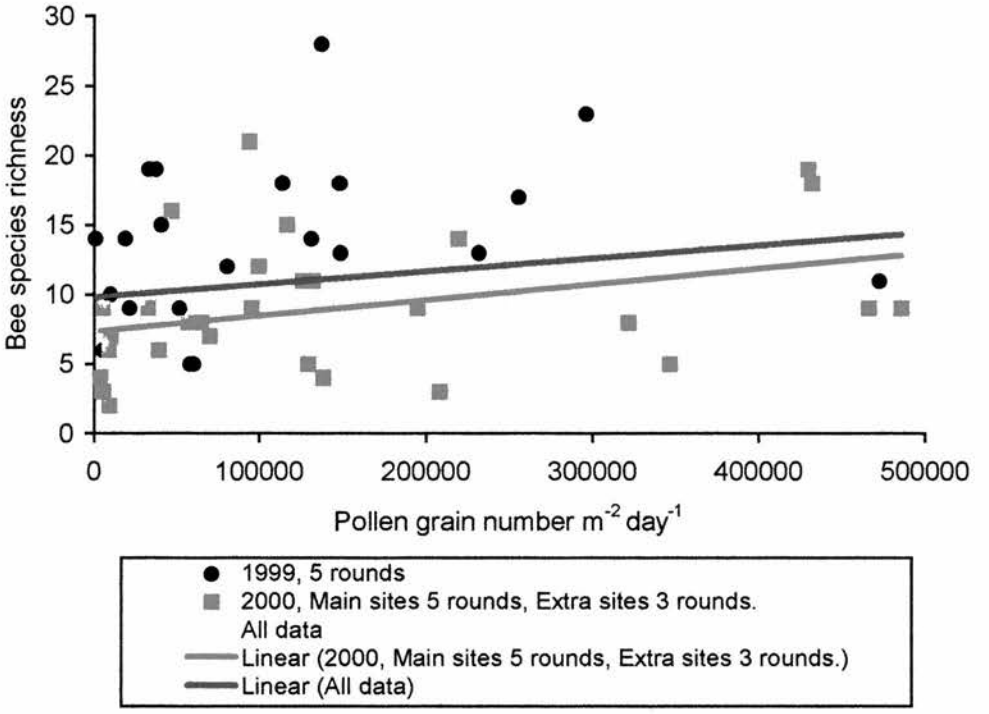


Figure 3.18: The relationship between bee species richness and pollen grain number across 2 years using all the available data.

Pollen grain number appears to have a much clearer positive effect on the bee community than does pollen volume. This may be due to inaccuracy in the methods used to measure grain size (some grains were squashed under the weight of a coverslip and therefore appeared larger than they really were, see chapter 2, section 2.1.5 f). Another possibility is that nutrient value of a pollen grain is not proportional to its size, and therefore that smaller grains have relatively higher amounts of energy or other useful nutrients, as is discussed in Section 3.5.

3.4.2.c) Pollen grain size

Pollen grain size did not affect bee abundance (SROC: r_S=-0.183, n=21, P=0.428) or species richness (SROC r_S= -0.306, n=21, P=0.177) in 1999, but both parameters showed negative trends with grain size in 2000 (Abundance; SROC: r_S= -0.439, n=30, P=0.015, Species richness; SROC: r_S= -0.372, n=30, P=0.043) and with the two years

combined (Bee abundance, Figure 3.19, SROC: r_S= -0.287, P=0.041, n=51, Bee species richness, Figure 3.20, SROC: r_S=0.078, n=51, P=0.587) although none of these trends were significant after Bonferroni adjustment.

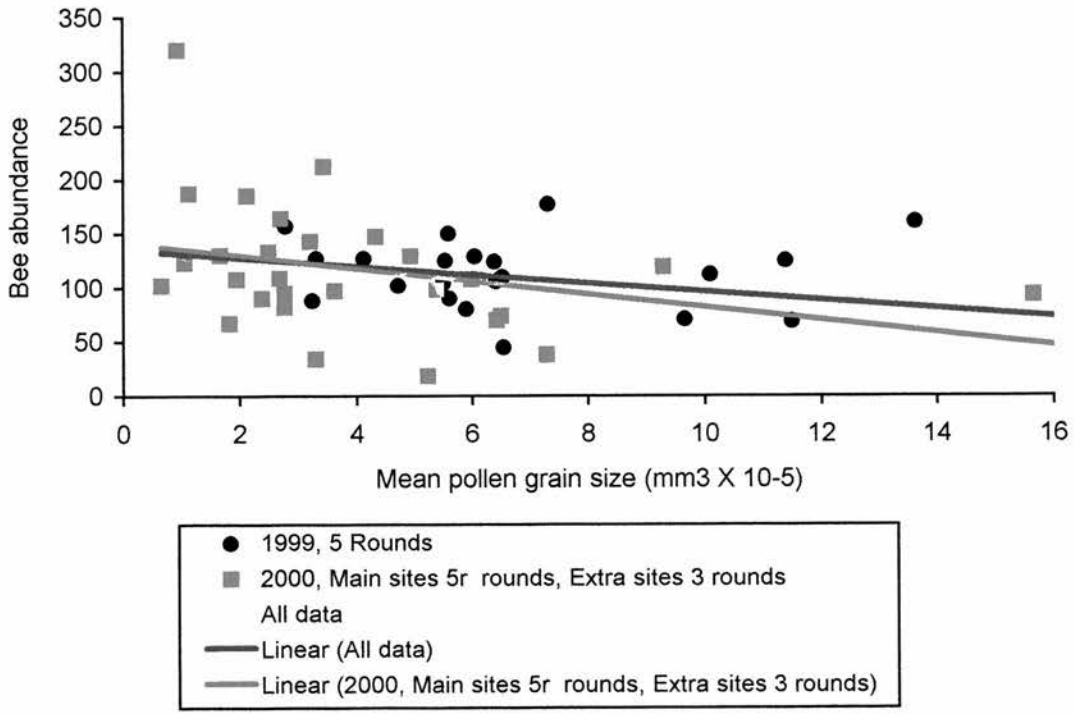


Figure 3.19 Pollen grain size related to bee abundance in both years

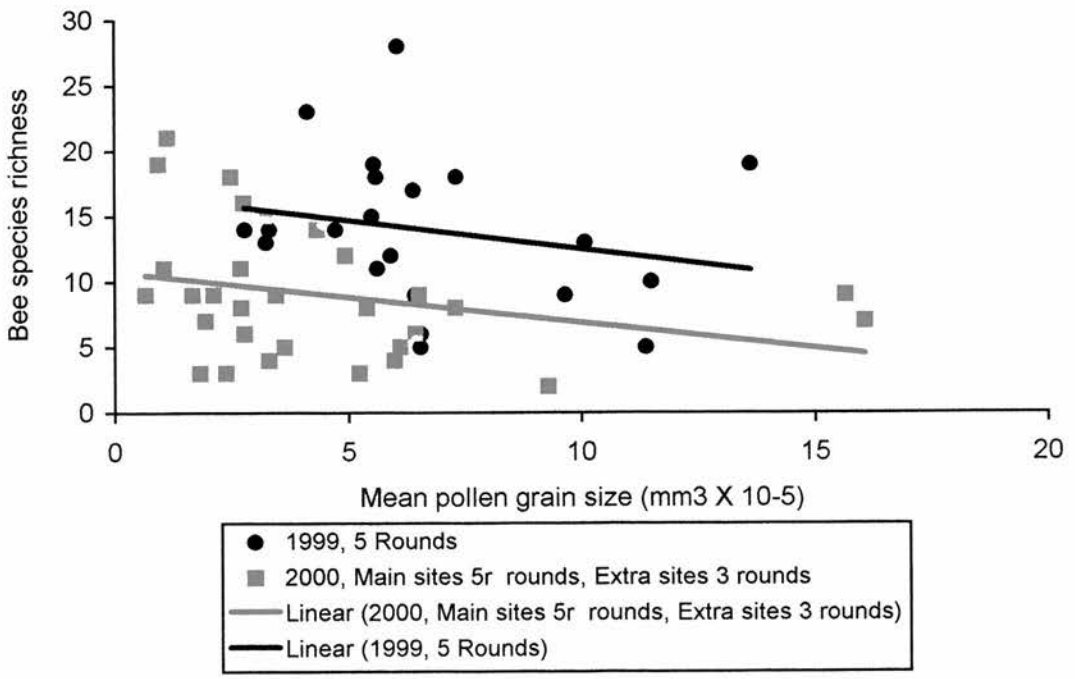


Figure 3.20 Pollen grain size related to bee species richness in both years

Thus there did seem to be a negative effect of grain size on bees. This may have been due to differences in proportional nutrient content of smaller grains, or to the ease of collection by bees. However it may simply have been because the plants with the smallest grains were mainly annuals and these had higher numbers of grains in each flower as well as more flowers overall, so grain size tended to decrease as total grain number increased (SROC: r_S=-0.287, P=0.041, n=51) as in Figure 3.21.

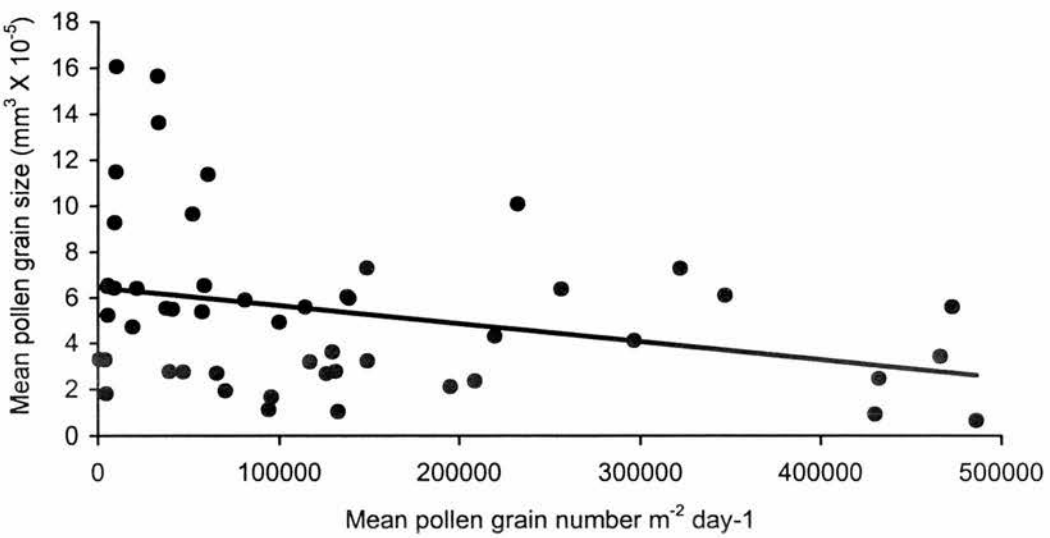


Figure 3.21 The mean size of a pollen grain related to the mean number of pollen grains in a plot.

3.4.3 Total energy

Values for pollen energy were estimated using pollen volume as described in Chapter 2. The mean pollen energy was 0.756 (±0.114) kJ ha^{-1} day^{-1}, much lower than the values for nectar energy, which averaged 23.433 (±5.304) kJ ha^{-1} day^{-1}; So values for nectar energy per unit area, averaged 93.61 times as high as those for pollen energy (Figure 3.22). Hence the values for total energy (nectar + pollen) had an almost identical pattern to those for nectar energy. Total energy therefore, was not looked at in detail.

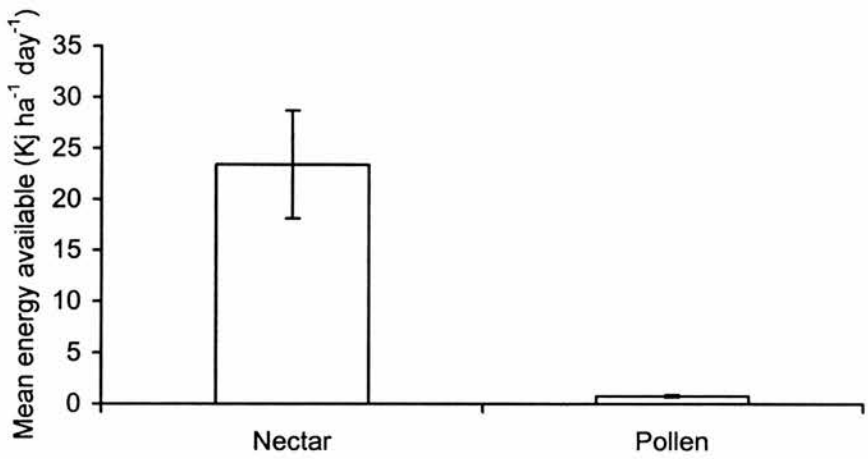


Figure 3.22 Mean amount of energy per unit area across both years.

3.4.4 Summary of section 3.4

	Bee abundance			Bee species richness		
	1999	2000	Both	1999	2000	Both
Nectar energy	0.021	>0.05	>0.05	>0.05	0.016	>0.05
Nectar water	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
Pollen volume m^{-2}	>0.05	0.032	0.027	>0.05	>0.05	0.03
Pollen grain number	>0.05	**<0.001**	**<0.001**	>0.05	0.028	0.029
Pollen grain size	>0.05	0.015	0.041	>0.05	0.043	>0.05

Table 3.7 Summary of the relationships between floral rewards and bee communities. Figures show P values. Those in Bold are still significant after SBA.

- Nectar had much higher energy values per unit area than pollen did.
- The only potential relationship between bees and nectar was a positive but non-significant trend between nectar energy and bee species richness in year 2000. However Potts *et al.* found that bee species richness was also related to the diversity of nectar niches.
- Species richness and abundance of bees tended to increase with both the volume of pollen available and the number of pollen grains. However the only significant relationship was that between pollen grain number and bee abundance.

- Bee abundance and species richness showed decreasing trends with pollen grain size but probably due to the negative relationship between grain size and abundance of annuals.

3.5 Discussion of Chapter 3

3.5.1 Flowers

Overall, the species richness and abundance of bees increased with species richness and abundance of flowers, and herb flowers were more important than shrub flowers. Bee species richness was best explained by flower species richness, whereas bee abundance was dependent mainly on total flower cover. This agrees with findings in set-aside fields and orchards in Germany (Steffan-Dewenter & Tscharntke 2001). The clear relationship between bee species richness and the species richness of flowers supports the prediction that the diversity of consumers is a function of the diversity of resources available (MacArthur 1972) and also fits with the assumption that the species richness of flowers is a good indicator of the diversity of resources they provide (varying both in nutrition and in accessibility). The total abundance of flowers also played a part in determining the species richness of bees, probably due to (a) the fact that where flowers are abundant, there are greater possibilities for the partitioning of resources between bee species and to (b) the close relationship between flower species richness and flower abundance.

It is important to know that bee species richness was limited by flower species richness rather than abundance because although in this study abundance and diversity of flowers were closely linked, systems do exist where there are large quantities of

flowers but few species. For example a monoculture of crops, or a heavily grazed, nitrogen rich area (as described in Chapter 4), may have large numbers of one flower species and therefore support large numbers but few species of bees.

The fact that herb flowers played a more important part than shrub flowers is partly because the majority (69 ± 5 %) of species were herbs, and therefore removing the shrub species from the analysis made little difference to the overall diversity in many sites. In sites dominated by shrubs one dominant species tended to take over, and therefore the overall diversity of flowers was low. For example at Haibar Nature Reserve, 99 (±1) % of flower cover consisted of shrubs, and 54 (±2) % was *Cistus salvifolius*. Steffan-Dewenter & Tscharntke (2001) showed that bees visited annuals more often than expected for their flower cover, whereas perennials were visited less often; thus bees probably do show a preference for annuals, and did not just use them more due to their high abundances.

The relationship between the abundance of bees and that of herbs must therefore mean that the majority of bee species were dependent on herbs (most of which are annuals) rather than shrubs. This may help to explain why pollen seems to be the main reward in phryganic systems (Herrera 1985; Petanidou & Vokou 1990) since annuals may often provide more pollen than nectar rewards (e.g. Fussel & Corbet 1992). Annual plants do not have large, established root systems and may therefore be less able to make use of what little water is available than perennials are, meaning that nectar must be very costly to produce in an arid environment, as is discussed later.

The abundance of bees was dependent mainly on the total flower cover and therefore on the total quantity of rewards available. Species richness also played a part in

explaining bee abundance, but since abundance and species richness of flowers were so closely linked, it was not possible to be sure which was the limiting factor. One would need to contrast very depauperate habitats, with large numbers of one flower species with areas where flowers were diverse but few in number, in order to really separate these two variables.

The abundance of bees present at one time is mainly the product of rewards available for investment in young from the previous years' flowers, as suggested by Tepedino and Stanton (1981). Since bee abundance was better explained by the flowers available in both years than in 1999 only, some bees must also have been attracted from elsewhere, into the current floral communities. Bee species richness, on the other hand, was mainly determined by flower species richness in the present year. Even if the bees present were entirely the product of the resources available in the previous year, their numbers would be bound to correlate well with the numbers of flowers in the present year because the two study years were very similar. As noted by Tepedino and Stanton (1981), the effects of floral resources in two different years would show up more clearly in a system where 'good' and 'bad' flower years alternated.

3.5.2 Nectar and Pollen

Bee species richness seemed to increase with nectar energy slightly in 2000, but not significantly, and otherwise nectar had no obvious relationship with bees. It may therefore be that the total amounts of energy and water provided by nectar do not limit these bee communities, but that the diversity of nectar resources does, as found by Potts *et al.* (Manuscript in submission), described in Section 3.4.1. Although the Potts *et al.* analysis looked at the variation in nectar types available to bees, it did not take

into account the diversity of floral structures or phenology. Another way to look at the diversity of nectar resources may be simply to look at the species richness of only nectar-producing flowers, which would indicate the diversity of structures, phenologies and nectar types all at once. However, simply taking the overall diversity of flower species seems to be a good way to get an overall measure of the diversity of rewards, taking into account both pollen and nectar at once, and as mentioned earlier, gave very good correlations with bee species richness.

The only significant relationship between bees and pollen was that between bee abundance and grain number. That the number of pollen grains had more effect on bee abundance than on bee species richness makes sense, since the total number of grains relates only to the total quantity of resources available, and not to their diversity. The fact that the number of pollen grains better explained bee abundance than the volume did, may be partly due to errors in measurement of grain volume, as described in Chapter 2 (Section 2.1.5), or else because of variation in the proportions of different nutrients that pollen grains contain. For example, pollen grains from different species vary in the relative amounts of lipid and carbohydrate they contain (Baker & Baker 1983) and protein content of pollen ranges from 2.5% to 61% (Roulston & Cane 2000). Petanidou and Vokou (1990) also showed that the energy content of pollen from entomophilous plants was very variable, compared to that from anemophilous plants. Pollen grains may therefore vary in which bee species they are most useful to (Roulston & Cane 2000). Pollen grain volume is unlikely to be directly proportional to the amount of energy or any other nutrients contained. Petanidou and Vokou (1990) did find that visitor diversity correlated with pollen energy content. However they measured the actual energy content of the pollen, using a calorimeter,

and therefore got much more accurate measurements than those we obtained using grain volume.

Pollen grain number did limit bee abundance, therefore it seems that grain number must indicate the abundance of some nutrients useful to bees. However sites with large numbers of small grains were those with the most annual flowers and therefore the highest diversity, so it could still be the diversity of flowers which really explains the high abundance of bees in these areas. It has also been shown (Baker & Baker 1983) that small pollen grains (<25μm) are always rich in lipids, therefore they may provide a more compact form of energy than larger grains.

The total availability of pollen seemed to be more important to bees than the availability of nectar, in spite of pollen having far lower energy levels per unit area. This may be due to other nutrients (proteins etc.) contained in pollen (Baker & Baker, 1983; Petanidou and Vokou 1990; Roulston & Cane 2000). Also, all flowers contained pollen rewards so these were spread relatively evenly through the sites, thus a small sample was likely to be representative of the whole site. Plants with high nectar rewards, on the other hand, had a very clumped distribution so that samples were greatly influenced by the occasional large flowering shrub. This means that our sampling method was probably not detailed enough to get a proper measure of such a patchy resource. The fact that the distribution of nectar resources is so patchy may mean that those bee groups most dependent on nectar were also clumped in patches and therefore not sampled as consistently as those with a more even distribution.

It may be that in very dry climates such as this, nectar availability is very variable from day to day and greatly influenced by the weather (e.g. Corbet *et al.* 1979;

Willmer 1983; Petanidou & Smets 1996), as well as being variable spatially; therefore pollen is a more constant and dependable resource. This agrees with Herrera (1985) who suggests that, in southern Spain, low and variable levels of rainfall have acted against the selection of taxa producing nectar as the sole reward to pollinators. It also explains the low contribution of Lepidoptera (which cannot use pollen) in Mediterranean ecosystems, noted by Petanidou and Vokou (1990).

The spatial variability of nectar sources may be especially important for those bees unable to travel long distances to find food sources, and may matter less to social bees which are able to recruit foragers from a distance to a patch of high rewarding flowers. Even the highly social *Apis mellifera*, which are known to travel long distances (Srinivasan *et al.* 1998), did not seem to be nectar limited, yet this is not conclusive since *A.mellifera* distributions are likely to be dependent more on the distribution of bee hives than on any other factor.

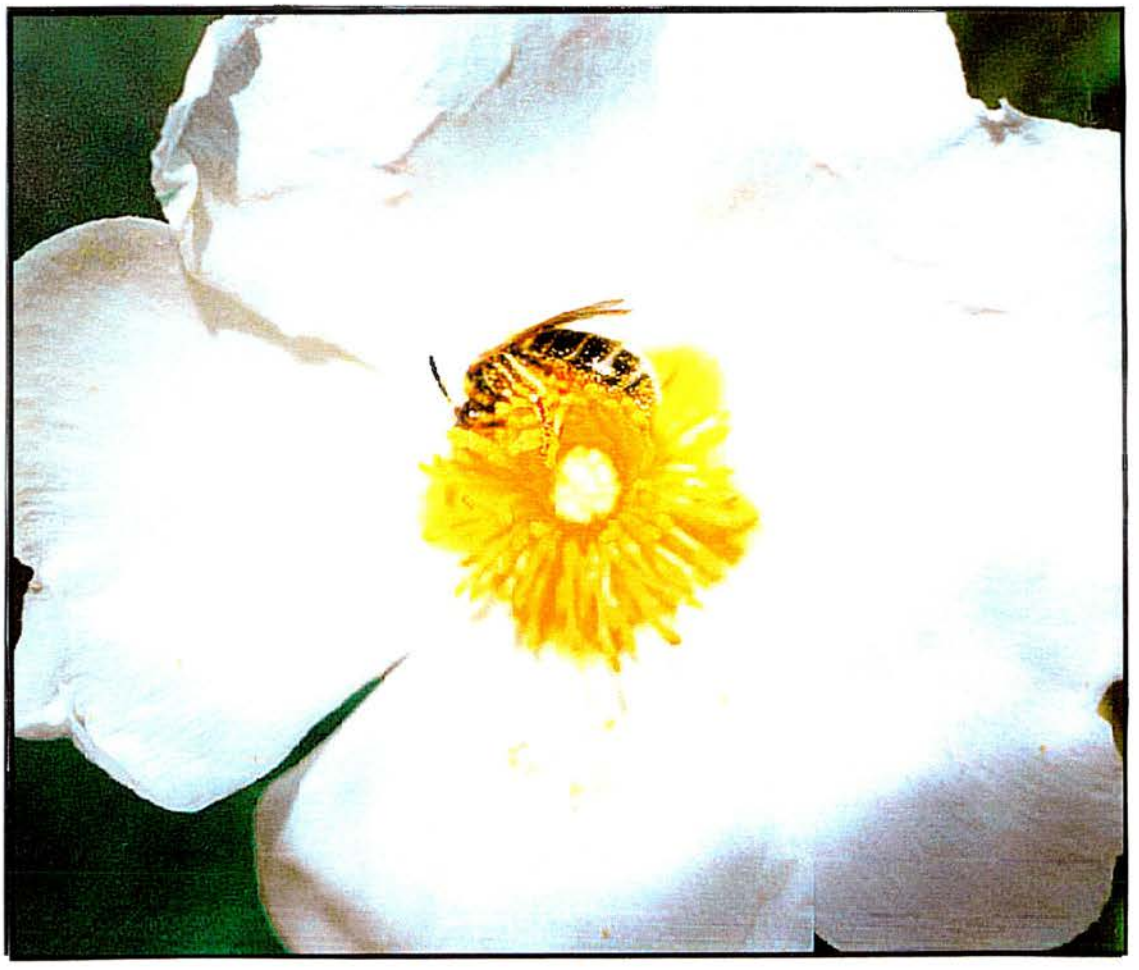
Since adult bees need an immediate source of energy (Simpson & Neff 1983) and also a source of water (Willmer 1986, 1988), it is surprising that the overall abundance of nectar appeared to have no effect on bee abundance. Sources of water might have been found elsewhere, although they must be hard to come by in such a dry environment. There were probably also significant amounts of both water and energy available from sources such as aphid honeydew which bees are known to collect (Whitfield, 2002), and from flowers producing very small volumes of nectar which we were unable to measure. For example in highly grazed sites the majority of flowers were composites such as *Chrysanthemum coronarium, Leontodon tuberosus* and *Silybum maritimum*. Many bees were seen visiting these (See Photographs 3.1 and 3.2) and were clearly collecting nectar, as well as pollen. However we were

unable to sample nectar from the tiny individual florets of composites, which may often produce large quantities of nectar (Proctor *et al.* 1996), and so probably underestimated the amount of nectar available at these sites. This means that grazing may be advantageous to bees if it increased the availability of composite nectar but there was not time during the present study to investigate this further.

Photograph 3.1 *Bombus sp.* visiting thistle flower in Greece.

Photograph 3.2 Halictid bee visiting *Calendula* sp. at Mitla, Israel.

Small amounts of nectar were also found in *Cistus creticus* and *Cistus salvifolius* which were until recently thought to produce pollen as a main reward and only negligible amounts of nectar (Herrera 1985; Proctor *et al.* 1996), yet small bees such as *Lasioglossum marginatum* made long visits to these flowers, and were definitely collecting nectar as well as pollen, since they spent most of their time below the anthers where the nectarines are (Photograph 3.3).



Photograph 3.3 Halictid bee collecting nectar from *Cistus salvifolius*.

Since these data were collected, Manetas *et al.* (2000) have re-examined *C. creticus*, (using rinsates of the flower interior and an enzymatic micro-assays of surface sugar) and found considerable amounts of sugar, yet only negligible amounts using the micro-capillary method.

It is certain therefore, that this study must have missed a considerable amount of nectar, though we did obtain a sub-sample of the types of nectar available across sites. However the methods of measuring very small volumes of nectar are extremely time consuming, and would not be feasible for a large scale study like this, unless a huge amount of man-power was available. However this means that the abundance and species richness of bees (which have been shown here to be closely related to the overall abundance of flowers), may indeed be limited by the availability of nectar although this study was not detailed enough to show it.

To summarise; this chapter shows bee species richness is dependant mainly on the species richness of flowers in the present year and bee abundance depends on the previous year's floral abundance, herbs being particularly important. The overall availability of pollen seems more limiting to bees than does any measure of nectar, which might be (a) because pollen is more available and less variable in such a dry environment, (b) because the diversity of nectar types is more important than their abundance, or (c) because many flowers produce nectar which is easily available to bees but difficult to sample.

4 Intensity of cattle grazing on Mount Carmel, and its effects on the diversity and abundance of flowers and bees

4.1 Introduction

Several previous studies linking bees and large herbivores, on Californian pumice flats (Sugden 1984), in the succulent Karoo of S. Africa (Gess & Gess 1983), in Swedish pastures (Soderstrom *et al.* 2001) and in British farmland (Fussel *et al.* 1991), have shown that grazing has deleterious effects on bee communities. However, it has been suggested that in the Mediterranean, grazing may also have positive effects (Petanidou & Ellis 1996) since it creates a heterogeneous shrub layer and opens up areas of bare ground, in which many bees prefer to nest (Wesserling and Tscharntke 1994).

The mechanisms through which grazers might affect bees include trampling, defoliation, defecation and urination. Trampling may damage nests or potential nest sites (Gess & Gess 1989; Sugden 1985), or else increase areas of bare ground which can be used for nesting (Petanidou and Ellis 1996). Trampling, defoliation and defecation may all cause changes in the structure and composition of vegetation and therefore in the food supplies and shelter available to bees. The detrimental effects of trampling suggested above seem likely only to occur at very high grazing levels, whereas trampling at moderate levels may be advantageous to bees.

The possible effects of grazing on vegetation are discussed in detail in Chapter 1 and include changes in the abundance and diversity of different plant species and in the structure of the vegetation. The relationships between grazers, bees and structural

heterogeneity will be investigated in Chapter 5. This chapter will concentrate on the changes in diversity and abundance of flowers due to grazing, and the way this affects bee communities.

Since it has been shown in Chapter 3, and in previous studies (Heiathus 1974; Moldenke 1975; Gathmann *et al.* 1994), that the structure of bee communities is very closely linked to that of floral communities, I expect bee diversity and abundance to follow a similar pattern to floral diversity and abundance.

There is a huge amount of literature from all over the world looking at the relationships between grazing animals and flora. Both the abundance and diversity of flowers can be increased or decreased by grazing depending on the species of grazers, the intensity of grazing, and the history of grazing in a particular habitat. Overall, it seems that floral diversity is likely to follow the intermediate disturbance hypothesis (Connell 1978, see also Paine 1966, 1971; Huston 1979) and be highest at intermediate grazing levels. However in parts of Israel, where there has been a long history of domestic grazing, the community includes many "grazing-adapted" plant species (Naveh & Whittaker 1979a) which are only negatively affected by very heavy grazing. In such studies the highest plant diversity was still found at an intermediate grazing level, but the optimum grazing level was much higher than in habitats with a shorter grazing history (Naveh & Whittaker 1979a; McIntyre *et al.* 1996).

Changes in the abundance of flowers are harder to predict than changes in diversity since there have been few studies of flower abundance across whole habitats. Studies of individual species have shown either increases or decreases in the number of

flowers produced following grazing (Anderson *et al.* 1994; Milton 1994; Noy-Meir & Briske 1996; Damhoureyeh & Hartnett 1997; Bergamier 1998; Kirby 2001). Floral abundance was correlated with floral diversity (Chapter 3) so they are likely to both react in similar ways to grazing. At high grazing levels though, when only a few grazing-adapted plant species remain (Naveh and Whittaker 1979b), these plants will have little competition and possibly high nutrient levels (due to herbivore dung) so may be very prolific and produce larger numbers of flowers than when they are competing with other species.

It is therefore expected that the diversity and abundance of both bees and flowers will peak at an intermediate level of grazing, but that this level may be relatively high, compared to areas where the vegetation is less well adapted to grazing. It is also likely that the maximum abundance of both bees and flowers will occur at a higher level of grazing than is the optimum for diversity.

In this chapter, I first explore the possibility of estimating the age of dung samples using their densities, and then describe the grazing regimes in the study areas on Mount Carmel across two years. Next, I investigate the effects of grazing on the diversity and abundance of flowers and bees, having accounted for variation caused by the differences in post-burn age across sites. Finally, I examine how particular families, or dominant species, of bees are affected by grazing, and look briefly at the mechanisms by which these effects take place.

4.2 Analysis of grazing levels

4.2.1 Dung decay experiment A:

In April 1999, ten fresh dung pats were marked and their weights and volumes were recorded every 10 days. The aims of this experiment were to find out how long dung could last in this environment and to see whether it would be possible to use the density of a dung sample to estimate its age.

Dung weight decreased by 65% in the first week of the experiment and continued to decrease until about day 15, thereafter remaining fairly constant at 80% of its original weight (Figure 4.1a). Dung volume also dropped rapidly at the start, decreasing by 29% in the first 15 days (Figure 4.1 b). However it did so relatively more slowly than dung weight, so that the density also went down by 71%, as shown in Figure 4.1(c), and then levelled out after about 15 days. It seems likely that density remained constant thereafter. However, this is not known since the experiment was trampled by cattle. Those dung samples not destroyed were still present 13 months later.

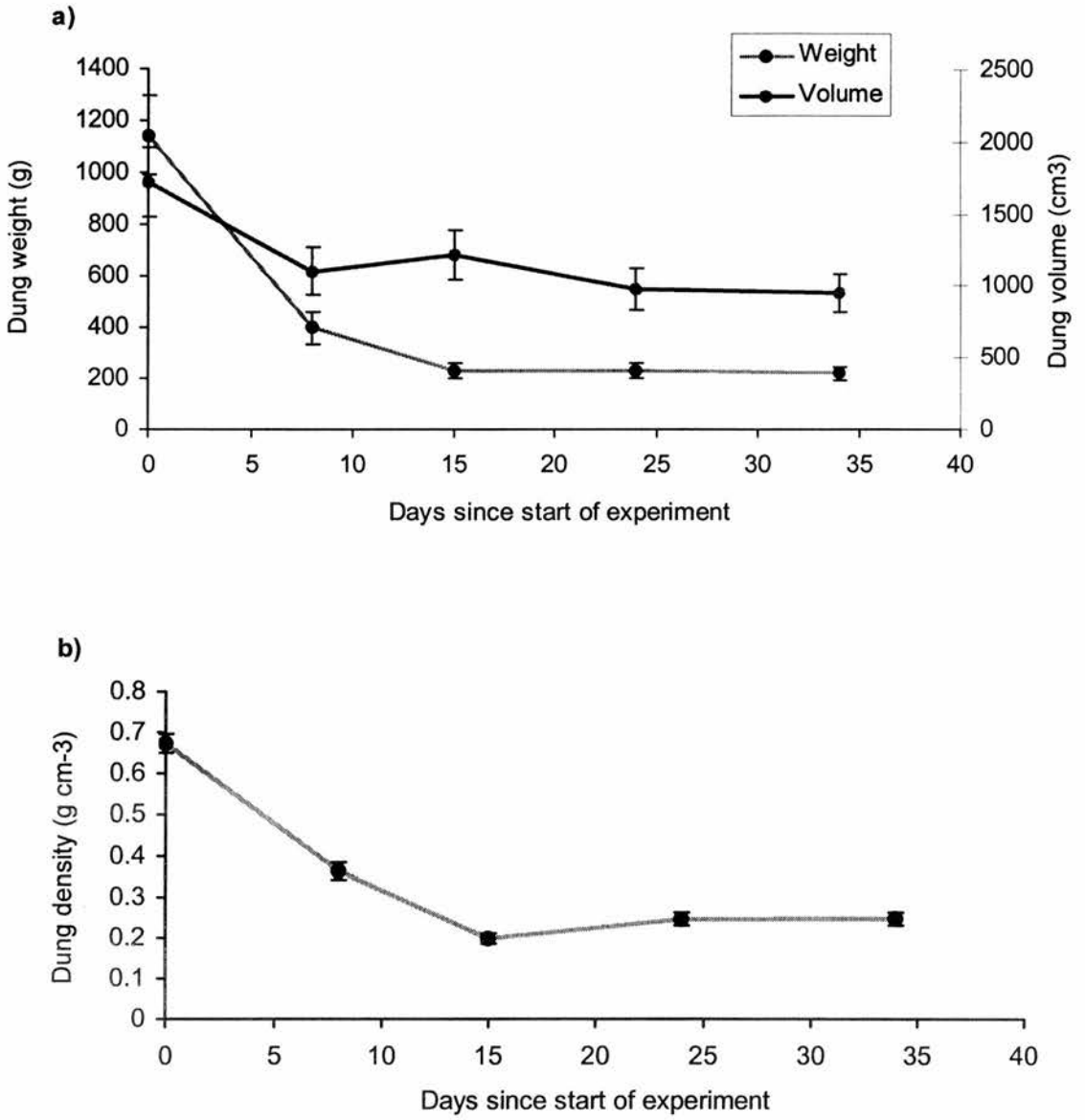


Figure 4.1. a) Change in mean dung weight and volume, b) Change in mean density. All for ten cow pats over time with standard error bars.

It is likely that some dung would always be destroyed by trampling. However the samples in Experiment A were placed in an open field which was more intensively used by the cattle than other areas. In Experiment B, the samples were left where they were found. This meant that some were in areas of scrub, which were less likely to be disturbed by cattle.

4.2.2 Dung decay experiment B

Ninety percent of the dung pats marked in April 2000 were still present in both Mit field and Mit Bot on leaving Israel in June 2000. These would have been recorded again in May 2001 but we were unable to return to the field sites. In February 2002, S. Potts recorded that much of the dung had again been trampled and some markers were not found, but a small amount of dung was still present showing that some dung can last at least 22 months in this habitat. This means that grazing levels recorded using dung counts are a reasonable measure of grazing up to 22 months ago and perhaps longer. It is not possible to tell when grazing took place during this time, but according to the farmers grazing levels in the most intensively grazed sites had remained the same for at least ten years, although the cattle could move where they liked within the sites (see questionnaires).

4.2.3 Questionnaires

The two farmers working at the heavily grazed sites were given questionnaires as described in Chapter 2. Their answers were descriptive rather than quantitative and are summarised here.

At all the Mitla sites, 50 cattle had been kept permanently for 10 years. Prior to this there had been no grazing since the fire in 1983. The cattle remain in the area all year round but can move where they like within the 500 ha and are given additional food in the summer and winter. The water trough is visited on every single day when there is no rain and therefore the area beside this (part of Shed 2), is very intensively trampled (this was also the area where dung counts were highest). Ein Hod is similar, having had 60 cattle for 40 years. However they are herded through rather than kept

permanently in the area, and are only grazed for 7 months of the year. No information was found for other sites as it was not known who used the land. However the maximum dung level at any other plot was 1.2 dung pats $100m^{-2}$ in 2000 and 1.1 dung pats $100m^{-2}$ in 1999. This is relatively very low as can be seen from Figure 4.2, and is probably the result of animals very occasionally being herded through the area.

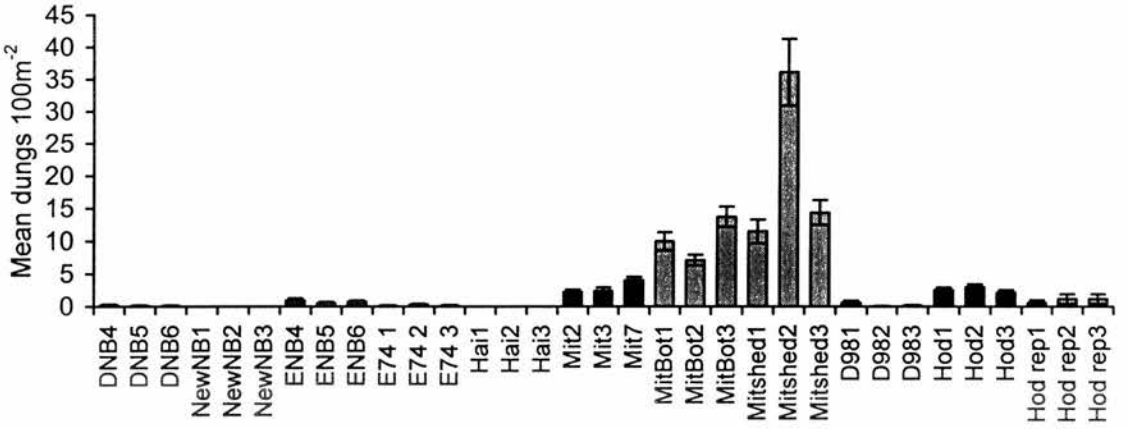


Figure 4.2. The mean number of dung samples per transect found in each site in order of decreasing time since burn. Black bars show means across 20 $100m^2$ transects for sites surveyed in both 1999 and 2000 and grey bars show means across 10 transects for those surveyed in yr 2000 only. Error bars show standard error.

4.2.4 Dung counts

Figure 4.2 shows the range of grazing levels in the sites surveyed in year 2000. In the sites used in 1999, dung levels were all low, ranging from 0 to 2.8 dung pats $100m^{-2}$. The extra sites surveyed in 2000 had dung levels of up to 36.1 dung pats $100m^{-2}$. However Shed 2 was still the only really intensively grazed plot due to the water trough in the middle of it. Otherwise the highest dung level was 14.4 dung pats $100m^{-2}$. The only totally undisturbed site was Haibar which is a Nature Reserve and entirely fenced off.

Dung levels in 2000 were found not to be correlated with time since fire (LR:

R^2=0.01%, n=30, P=0.548), therefore grazing and fire effects should be separable. However the only sites with moderate to high grazing levels were burnt in 1998 or 1983. Therefore, in sites of other ages, only the effects of very low grazing levels can be looked at.

Comparing dung levels for the two years (Figure 4.3) shows that they are generally similar but significantly increased in 2000 at Mit 3 (2 Sample T: T= -2.27, n=10, P=0.036), Mit 7 (T= -3.11, n=10, P=0.006) and Hod 3 (T= -2.33, n=10, P=0.032). Den 98 had some dung in 2000 and none in 1999 and DenNB which burnt down after 1999 had a little dung whereas NewNB, which was used in 2000 to replace it, had none. At all other sites levels were consistent between years, again indicating that dung counts are a reasonable measure of grazing intensity.

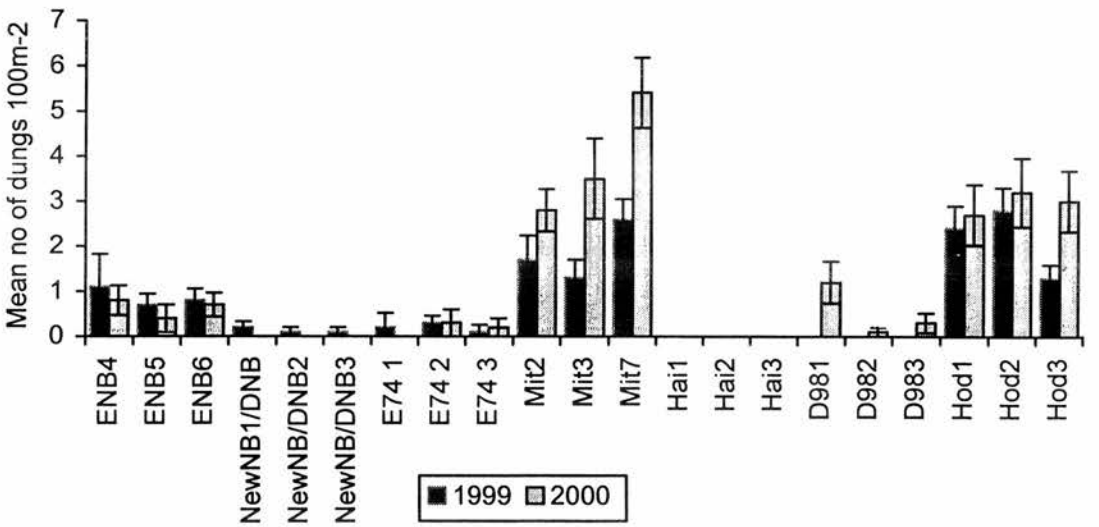


Figure 4.3. The change in dung levels from 1999 to 2000 at the 7 main sites. The point labelled NewNB/Den NB was DenNB which burnt down in December 1999 and was replaced with NewNB in 2000. Error bars show standard error across ten 100m^2 transects.

4.2.5 Summary of section 4.2

- Since the measured dung frequency in our sites matched well with information from farmers, it is assumed that dung counts are a relatively good method of measuring grazing intensity.
- Density cannot be used to estimate dung age, except to show whether it is more or less than 15 days old.
- Some dung does last for at least 22 months, so dung counts measure an element of the grazing levels across 2 to 3 years, although the majority of dung is from recent grazing.
- The increase in dung levels across the two years in some plots showed that the majority of dung counted must be from within the last year. Although the same number of cattle always had access to these areas, they could move freely within the sites and must therefore have chosen to spend more time in the survey plots during the second year.
- Dung counts can therefore be taken as a good measure of grazing levels during the past year, although grazing previous to this will raise the dung count.
- In those sites with moderate to high grazing levels, the number of animals in the areas has been the same for the last ten years. It is therefore assumed that the grazing levels measured have been similar for ten years.

4.3 Grazing levels and soil nutrients.

Soil in each plot was tested for Nitrogen, Phosphorus and pH. All values are shown in Table 4.1.

Plot	Nitrogen	Phosphorus	pH
Den98 1	Medium	Medium-Low	>7.5
Den98 2	Medium-Low	High	>7.5
Den98 3	Medium-Low	Low	>7.5
Hod1	Low	Medium	7.5
Hod2	Low	High-Medium	7.5
Hod3	Low	High	7.5
HodRep1	Medium-Low	Low	>7.5
HodRep2	Medium-Low	Medium	>7.5
HodRep3	Medium-Low	Low	>7.5
Haibar1	Medium-Low	High	>7.5
Haibar2	Medium-Low	High	>7.5
Haibar3	Medium-Low	High-Medium	>7.5
Mit2	Medium-Low	Medium-Low	7.5
Mit3	Low	High-Medium	7.5
Mit7	Medium-Low	Medium	7.5
Bot1	Medium	Medium	7.5
Bot2	Medium	Low	7.5
Bot3	Medium-Low	Medium	7.5

Plot	Nitrogen	Phosphorus	pH
Shed1	High-Medium	Low	7.5
Shed2	Medium-Low	Medium-Low	7.5
Shed2 (by water trough)	High-Medium	High	7.5
Shed3	Medium-Low	Low	7.5
Etz 741	Low	High-Medium	7.5
Etz 742	Medium-Low	Medium	7.5
Etz 743	Medium-Low	High-Medium	7.5
Etz NB4	Medium	Medium-Low	7.5
Etz NB5	Medium-Low	Low	7.5
Etz NB6	Medium	Medium-Low	7
NewNB4	Medium	High-Medium	7.5
NewNB5	Medium	Low	7.5
NewNB6	Medium	Low	7.5

Table 4-1 Nitrogen, Phosphorus and pH levels in all study sites.

The pH only varied from 7 to 8, but seemed to decrease with time since burn (Figure 4.4 a). The majority of plots had medium to low levels of nitrogen and only Shed 1 and the area of Shed 2 right beside the water trough (the most intensively grazed plots) had higher levels (Figure 4.4 b). Phosphorus levels were quite variable across sites. This seemed to bear no relation to grazing intensity (Figure 4.4 c), but phosphorus levels did tend to be higher in older sites.

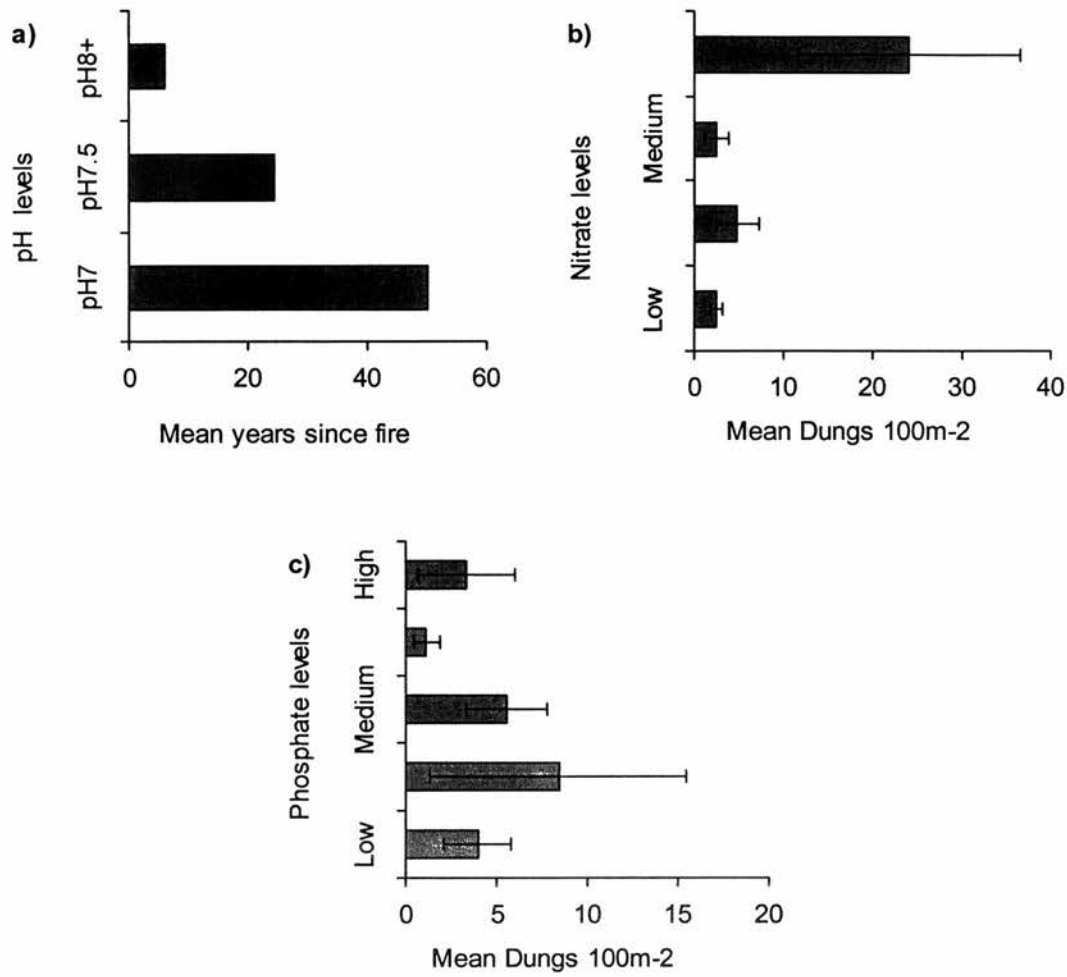


Figure 4.4 (a) pH plotted against site age. (b) Nitrogen and (c), phosphate levels plotted against grazing intensity.

4.4 The effects of grazing on the diversity and abundance of flowers and bees.

Sequential Bonferroni Adjustments were made according to the summary tables at the end of this section (Referred to hereafter as SBA).

4.4.1 Accounting for the effects of site age.

In order to investigate the specific effects of grazing on bees and flowers, adjustments were made to account for the effects of site age. Mean values were plotted against

time since fire, using only those sites with little or no grazing (less than 1 dung sample/100m^{-2}). This is shown for flower species richness in Figure 4.5.

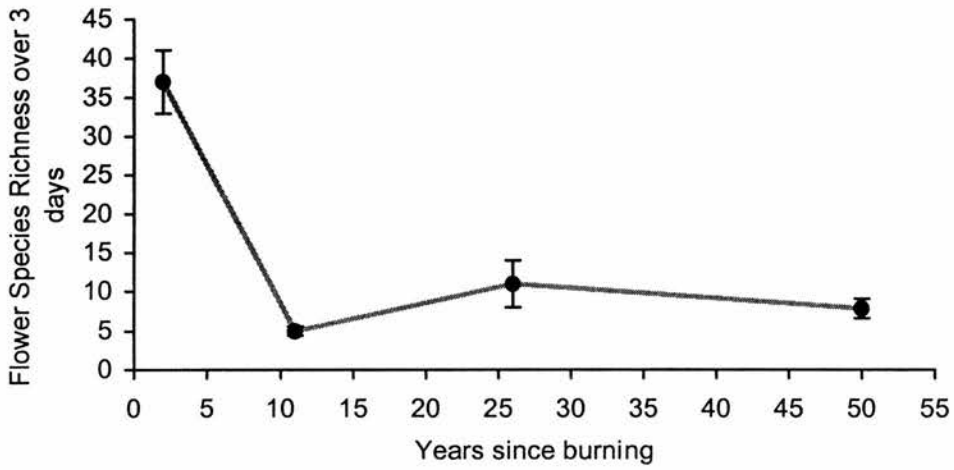


Figure 4.5 Flower species richness plotted against fire, using only those plots with less than 1 dung sample 100m^{-2}. Error bars show standard error across all plots of the same age. N.B, there is no data point for the 17 year old sites since none of them had less than 1 dung sample 100m^{-2}.

Values from these plots were then used to give a predicted level of abundance or diversity for a site of each age with little or no grazing. These values were then subtracted from the actual values in all plots of the same age, so that when plotted against grazing levels the intercept was brought down to zero. Real and adjusted plots for flower species richness are shown in Figure 4.6 a and b; with the adjustment, the data fall into a single, reasonably consistent relationship for the effects of grazing.

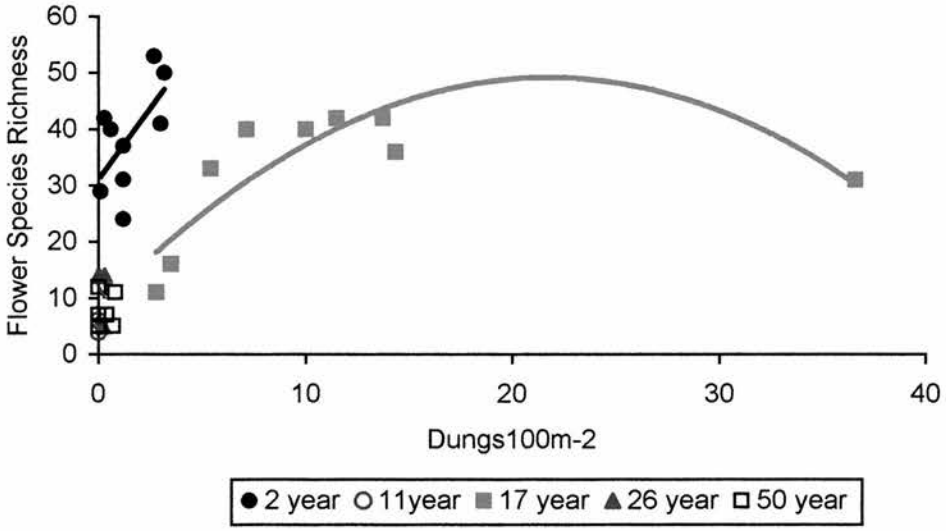


Figure 4.6 a) Actual values for flower species richness across 3 days in year 2000 plotted against mean dung levels. Legend shows years since burn. Points labelled as 50 years old, have not been burned for at least 50 years.

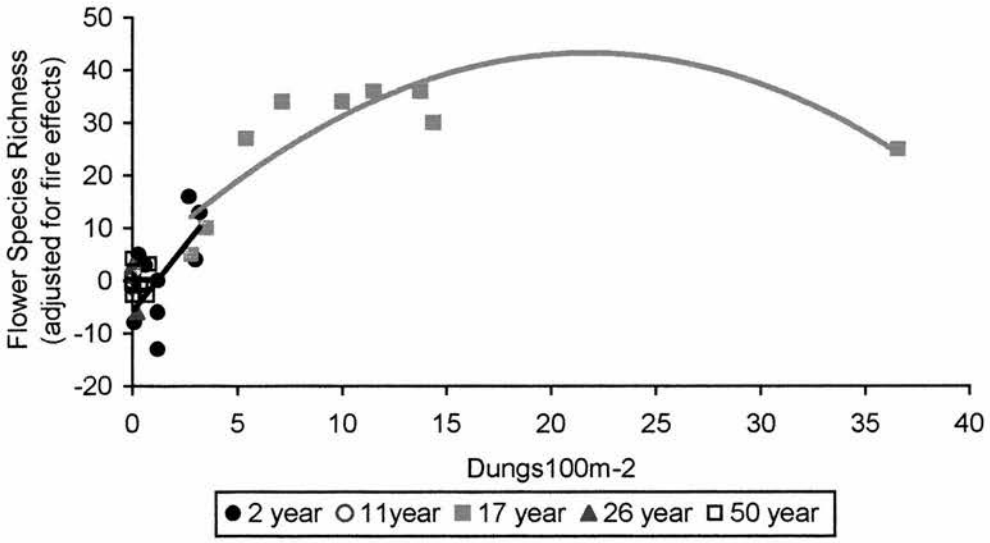


Figure 4.5 b) Real flower species richness, minus predicted flower species richness for no grazing, plotted against mean dung levels.

This technique therefore allowed the variation caused by grazing to be analysed without the confounding effect of extra variation caused by fire. Note however that the values shown in (b) are lower than any real values, and predicted values for any one site age would have to be added back on to give an idea of real values. Hereafter,

when this method is used, the data will be labelled "adjusted for fire effects".

4.4.2 1999 Results

After adjustment for fire effects, floral species richness was found to increase significantly with grazing intensity in 1999 (Figure 4.7; LR: R^2=44.6%, n=21 P<0.001). Furthermore, a positive trend was found for the relationship between floral abundance and grazing intensity (Figure 4.8: LR: R^2=17.8%, n=21, P=0.056) but this was not significant.

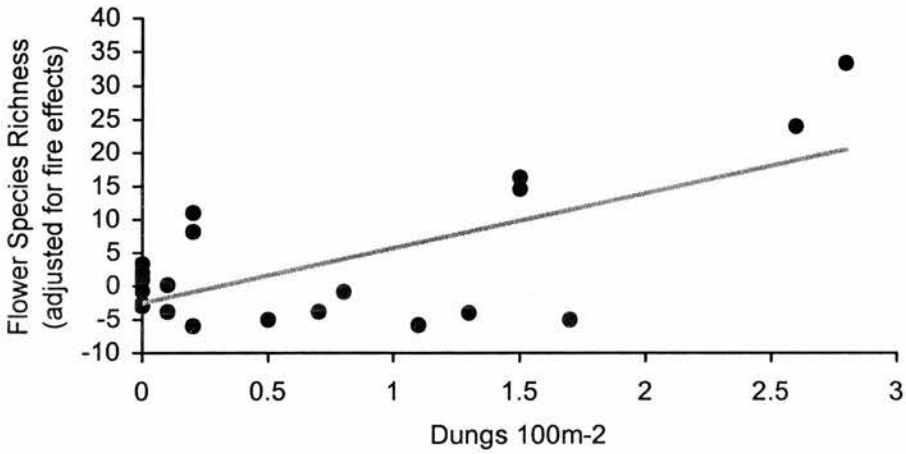


Figure 4.7. Flower species richness over 5 days in 1999 with grazing intensity.

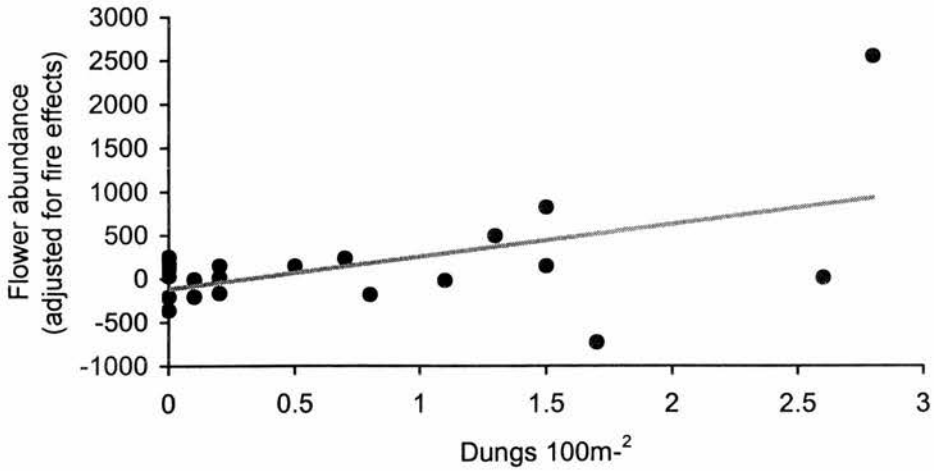


Figure 4.8. Flower abundance over 5 days in 1999 with grazing intensity.

However no significant relationships were found between bee species richness and grazing intensity (LR: R^2=0.1%, n=21, P=0.871) or bee abundance and grazing intensity (LR: R^2=1.8%, n=21, P=0.567) as is shown in Figure 4.9, (a) and (b).

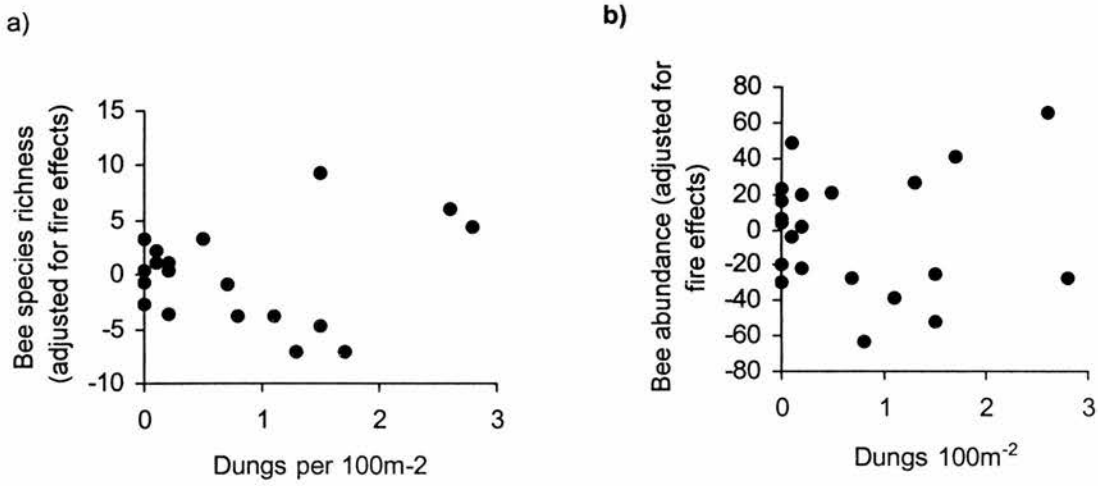


Figure 4.9 a) Bee species richness with grazing intensity in 1999, b) Bee abundance with grazing intensity in 1999. Each plot was surveyed on 5 days.

These results suggest that grazing has a positive effect on flower species richness and abundance but no effect on bee species richness or abundance. However, bee species richness and diversity correlate with floral species richness and diversity as shown in section 3.2. Grazing must therefore have some positive effect on bees, at least indirectly, and it may be that the grazing levels in the sites surveyed in 1999 were not high enough for this difference to be detectable. It was hypothesised in Chapter 1 that the species richness of bees and flowers would peak at intermediate grazing levels then decrease again. The sites surveyed in 1999 only had 1-3 dungs $100m^{-2}$, so it seems likely that only the first (increasing) part of this curve was measured and that none of the sites surveyed so far were "overgrazed" enough to reduce diversity again. During the second field season, extra sites were included with higher grazing levels.

4.4.3 2000 Results

4.4.3 a) Flower species richness

Data collected in the second field season show that the relationship between dung levels and flower species richness fitted a polynomial curve as in Figure 4.10 (PR: R^2=84.3%, n=30, P<0.001). F-Tests showed that this curve fitted better than either a straight line (F=59.01, DF=1,27, P<0.0001) a rectangular hyperbola (F=15.25, DF=1,27, P=0.0006) or an exponential curve (F=102, DF=1,27, P<0.0001). Although these results seem highly influenced by Shed 2, (the only really intensively grazed plot), the polynomial relationship persists even if this point is removed (R^2=84.5%, n=29, P=0.009). The open red square in Figure 4.10 shows an estimated point, which was **not** included in the analysis. It represents one area right beside the water trough in Shed 2, which was covered with a continuous layer of dung and had no flowers at all. No specific measurements were taken for this part of the site alone, but it does indicate what happens with extremely high grazing levels. (Parts of flower and dung transects crossing this area were excluded since dung samples could not be counted accurately).

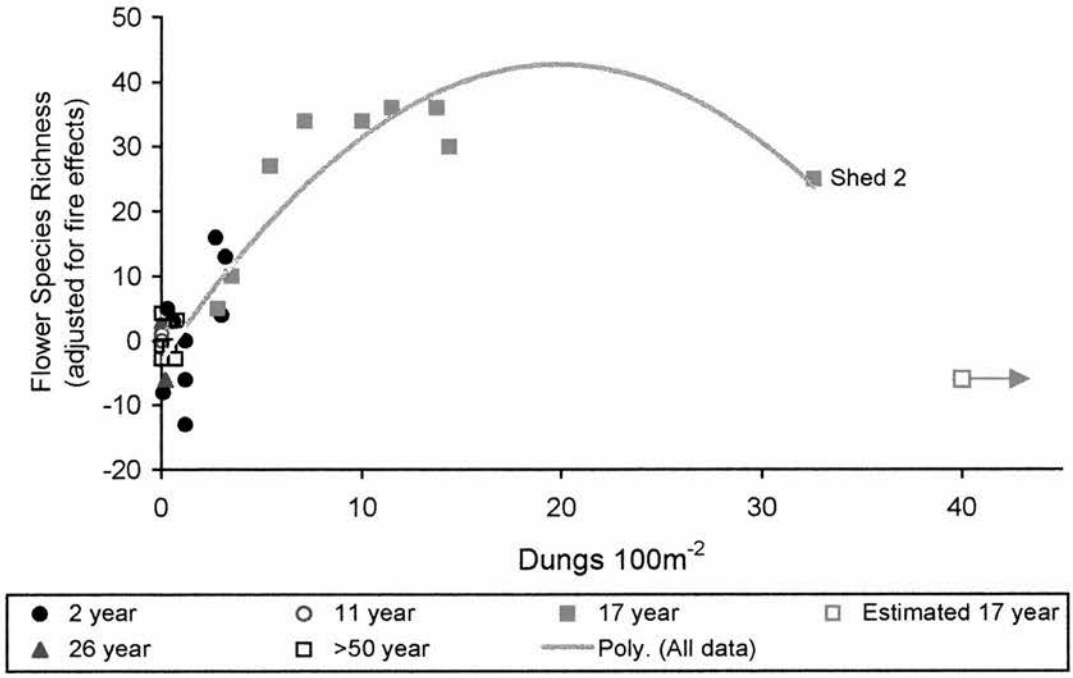


Figure 4.10 Flower species richness over 3 days (adjusted for fire effects) plotted against grazing levels in 2000. Grey line shows a polynomial curve through all data points.

When herb and shrub species were separated (using the data from 2000 only) it became clear that most of the increased flower species richness described above was made up of herb species. These fit a polynomial curve when plotted against grazing intensity (PR: R^2=0.658, n=30, P<0.001) and again, this curve fitted significantly better than either a straight line (FTEST: F=75.84, DF=1,27, P<0.0001), a rectangular hyperbola (FTEST: F=17.7, DF=1,27, P=0.0003) or an exponential curve (FTEST: F=125.1, DF=1,27, P<0.0001). However this was, again, highly influenced by the far right hand point (Shed 2), without which the data fitted a straight line (LR: P<0.001, R^2=82.7%, n=29). The species richness of shrub flowers tended to decrease slightly but this was not significant after SBA (SROC: r_S=-0.398, n=30, P=0.029) even without Shed 2 (LR: P=0.020, R^2=18.4%, n=29). Figure 4.11 shows both of these relationships. Since it was shown in Chapter 3 that bees were dependent mainly on herbs rather than shrubs, it seemed likely that bee species richness would follow a

similar pattern to that of herb flowers rather than shrub flowers.

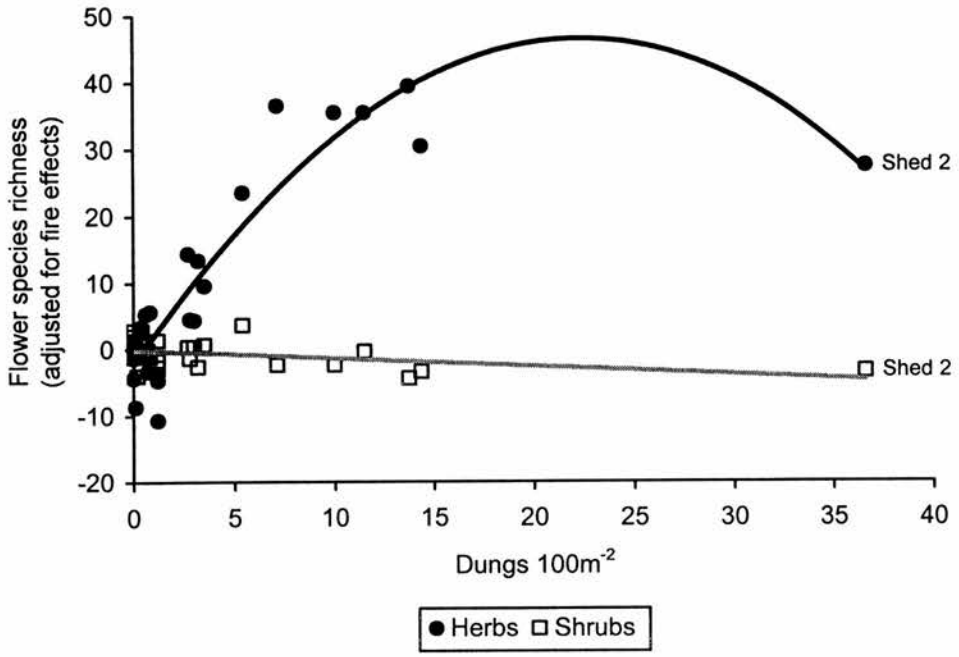


Figure 4.11 Shrub and herb species richness (adjusted for fire effects) related to grazing levels.

4.4.3 b) Flower abundance

For flower abundance and grazing levels (Figure 4.12), there was no significant relationship when all sites were combined (SROC: r_S-0.392, n=30, P=0.093). When the sites burnt 17 years before (these being the sites with the highest grazing levels) were analysed separately, floral abundance increased with grazing intensity (LR: R^2=79.9%, n=9, P<0.001), although this was not quite significant when Shed 2 was removed (LR: R^2=47.0%, n=8, P<0.061).

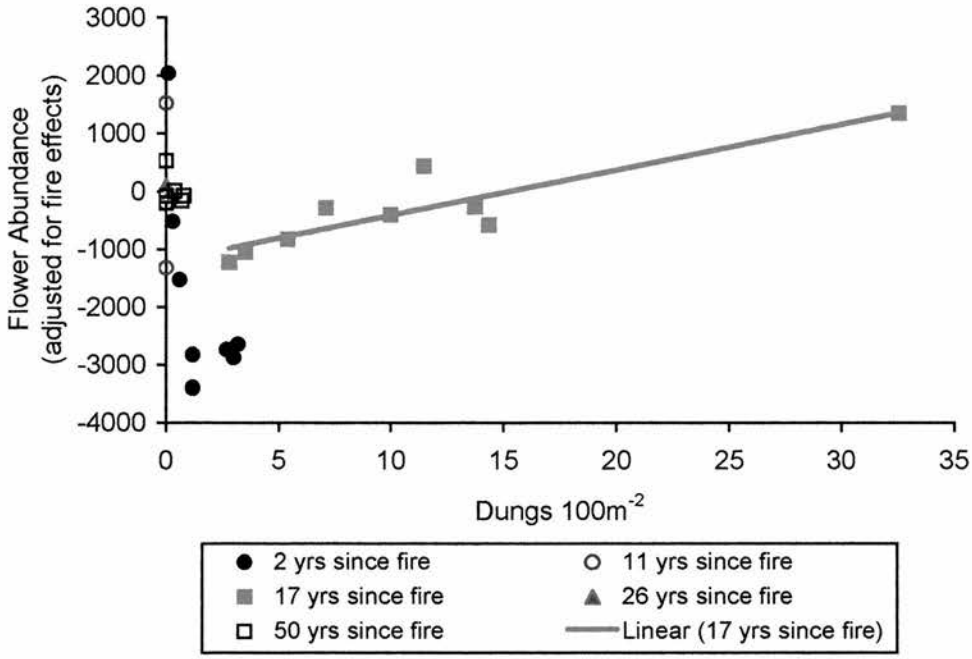


Figure 4.12 Flower abundance (adjusted for fire effects) plotted against grazing levels in 2000.

The abundance of flowers in the two year old sites (the only other sites with moderate grazing levels) was not obviously affected (LR: R^2=36.6%, n=9, P=0.085). This may be because grazing has less impact on recently burnt sites, which already have abundant flower cover. The abundance of some species may increase and others decrease, so that species composition is altered but the total number of flowers does not change. It may also be because flower abundance is less sensitive to grazing than species richness is. Species richness increases with grazing because some of the dominant species are removed and competition is increased. The overall abundance of any one species may increase due to reduced competition and increased nitrogen availability. However this would only happen at relatively high grazing levels, so the low grazing levels found in the two year old sites may not have been enough to have any effect on flower abundance.

When split into herbs and shrubs, the relationship was clearer. The abundance of flowering herbs (Figure 4.13) showed a positive trend with grazing levels (SROC: r_S=0.440, n=30, P=0.015) although this was not significant after SBA. The abundance of flowering shrubs decreased (SROC: r_S= -0.592, n=30, P=0.001) even without Shed 2 (SROC: r_S=-0.561, n=29, P=0.002). This means that when shrubs and herbs were added together (as in Figure 4.12) there was only a slight increase in flower abundance overall.

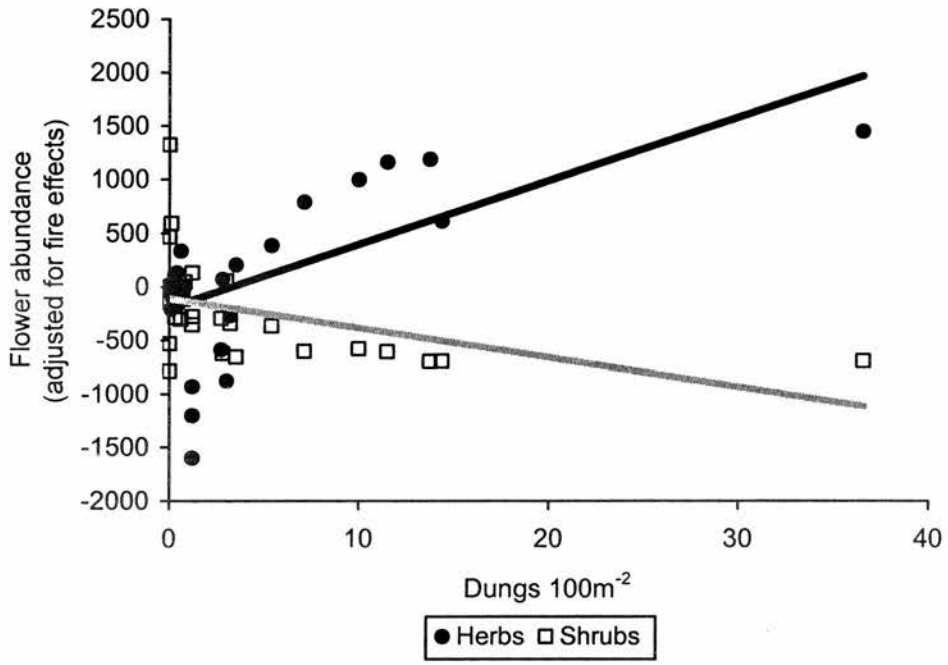


Figure 4.13 Abundance of herb and shrub flowers, plotted against grazing levels.

4.4.3 c) Bee species richness

The relationship between bee species richness and grazing levels fitted a rectangular hyperbola, Y=(7.469 x X)/(3.265+X), (r=0.6308, R^2=39.8%, DF=28, P=0.0002). This curve was fitted using "Graph Pad, Prism", and an R-value calculated using "Statistica". The rectangular hyperbola fitted better than a straight line

(R^2=20.63, DF=28), a polynomial curve (R^2=36.2%, DF=27) or an exponential curve (R^2=12.1%, DF=28). Since all other curves had equal or lower degrees of freedom and lower R^2 than the one-site binding hyperbola, F-Tests were not necessary in this comparison.

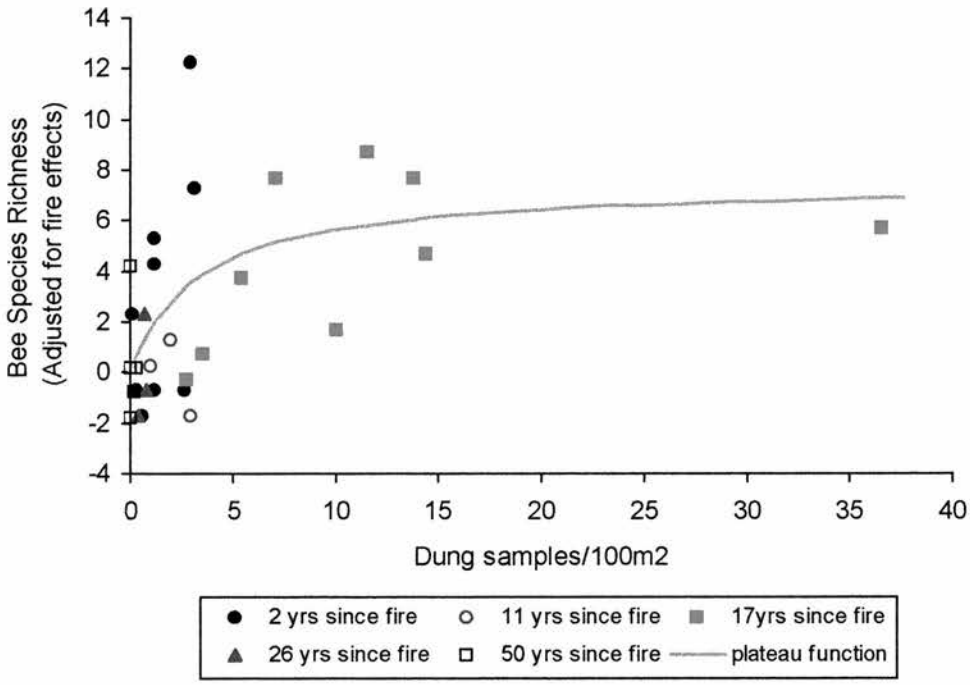


Figure 4.14 Species richness of bees in 2000 (adjusted for fire effects) related to grazing level.

It seems then that bee species richness increases with increasing grazing intensity, up to about 10 dung pats $100m^{-2}$ after which it begins to level out. However, since only one field site had more than 15 dung samples $100m^{-2}$, this is not certain. It is still possible that at even higher grazing levels, bee species richness would begin to decrease again as only a few, grazing tolerant plant species would remain. The optimum grazing level for flower species richness was at around 20 dungs$100m^{-2}$ (see Figures 4.10 and 4.11), but bee species continued to rise slightly at higher levels than this, probably due to other positive effects of grazing such as the increase in total floral abundance (see Figure 4.12) and availability of nesting sites.

4.4.3 d) Bee abundance

Figure 4.15 shows that bee abundance also increased with increasing grazing level (LR: R^2=57.7%, n=30, P<0.001) and showed no sign of decreasing again even at 36 dungs 100m $^{-2}$ (Shed 2).

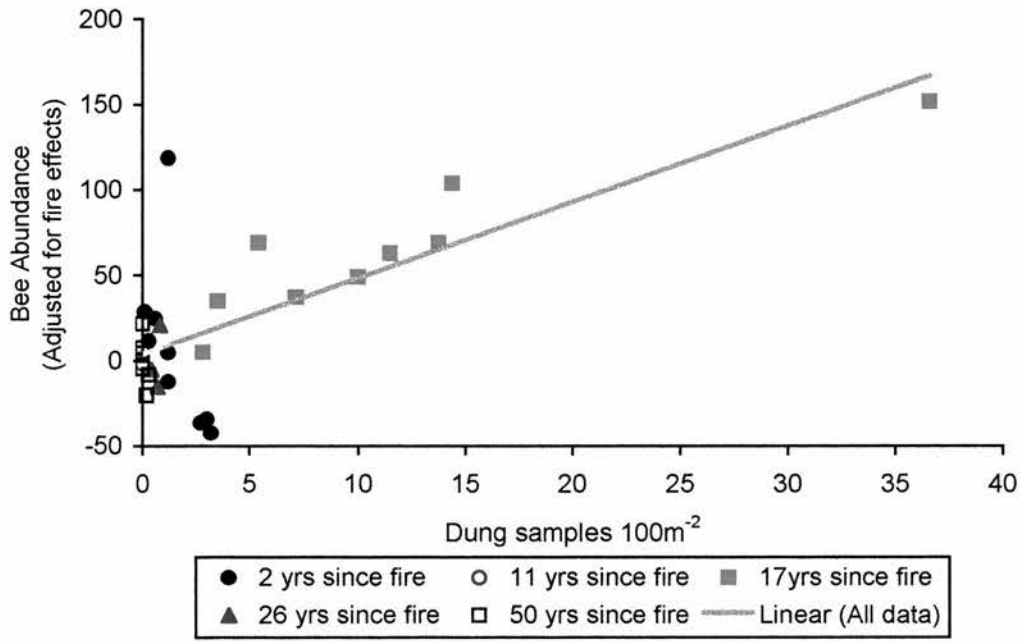


Figure 4.15 Abundance of bees in 2000 (adjusted for fire effects) related to grazing level.

This supports the suggestion made in Chapter 3, that floral abundance is the most important limit on bee abundance and that the species richness of flowers is less important. Other effects of grazing may also be important, such as a greater availability of bare soil for nesting.

4.4.4 Path analysis

Path analysis was used with the data from 2000 (3 days surveys at each site) to explore the relationships between burning, grazing and bees (Figure 4.16). See section 2.5.2 for further explanation. The log of dung levels was used to control for

the curved relationship between grazing and species richness. It was not possible with this technique to include two directional paths connecting herb species richness to herb abundance, or bee species richness to bee abundance, therefore conclusions should be viewed in the light of this.

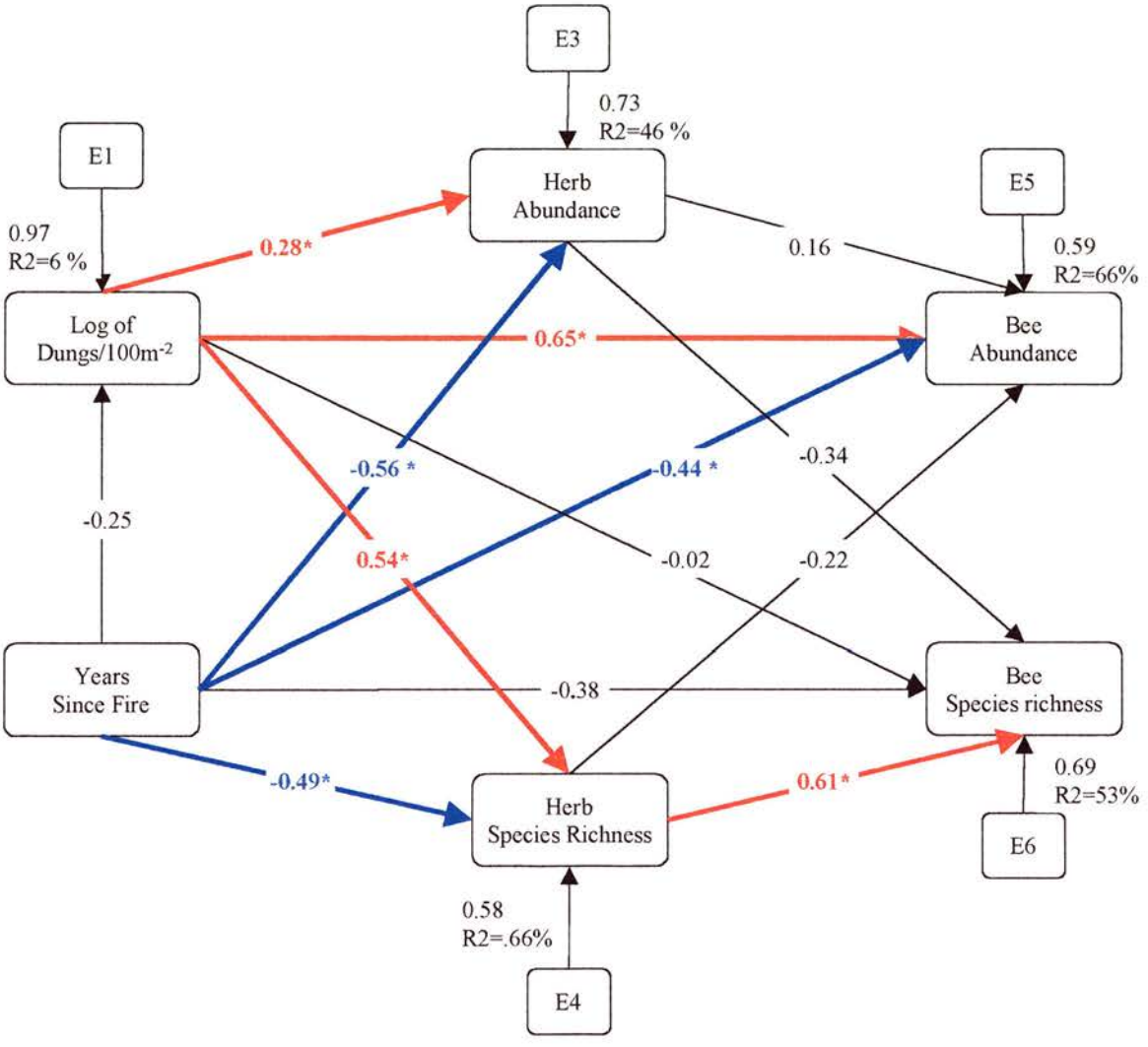


Figure 4.16 Path model constructed using EQS for windows. Shows the paths by which grazing and fire may affect the abundance and species richness of bees. χ^2=30.86, P<0.001, CFI=0.75, RMSEA=0.71. Values on diagram are partial regression coefficients. Those in blue show negative relationships and those in red show positive ones. Bold coloured lines show relationships which were significant at 0.05, and narrow black lines show insignificant relationships (>0.05).

The first model created, containing all possible links, (apart from those noted above), gave a high chi squared value (30.86) and a low P value (<0.001), showing that the observed data were significantly different from the model. If the model was a

good fit, RMSEA should also be <0.1 and CFI should be >0.90. However when the insignificant paths were removed, but a link was added between herb abundance and herb species richness, this gave a χ^2 value of 5.93 and a P value of 0.31. CFI was also close to 1 and RMSEA was <0.09, showing that the observed data were consistent with the new model (Figure 4.17). The path between the species richness and abundance of herbs could be put in the other direction, but this model was a poorer fit (χ^2=8.48, P=0.29).

This final model supported the proposition that grazing affects bee species richness by altering the species richness of herb flowers, rather than having direct effects. Fire also affected bee species richness but only very indirectly, via herb abundance then herb species richness. Surprisingly, the model also showed that the main effects of fire and grazing on bee abundance were not via the abundance of herbs. However grazing appears to have a direct, positive effect on bee abundance, and site age seemed to have a direct negative effect.

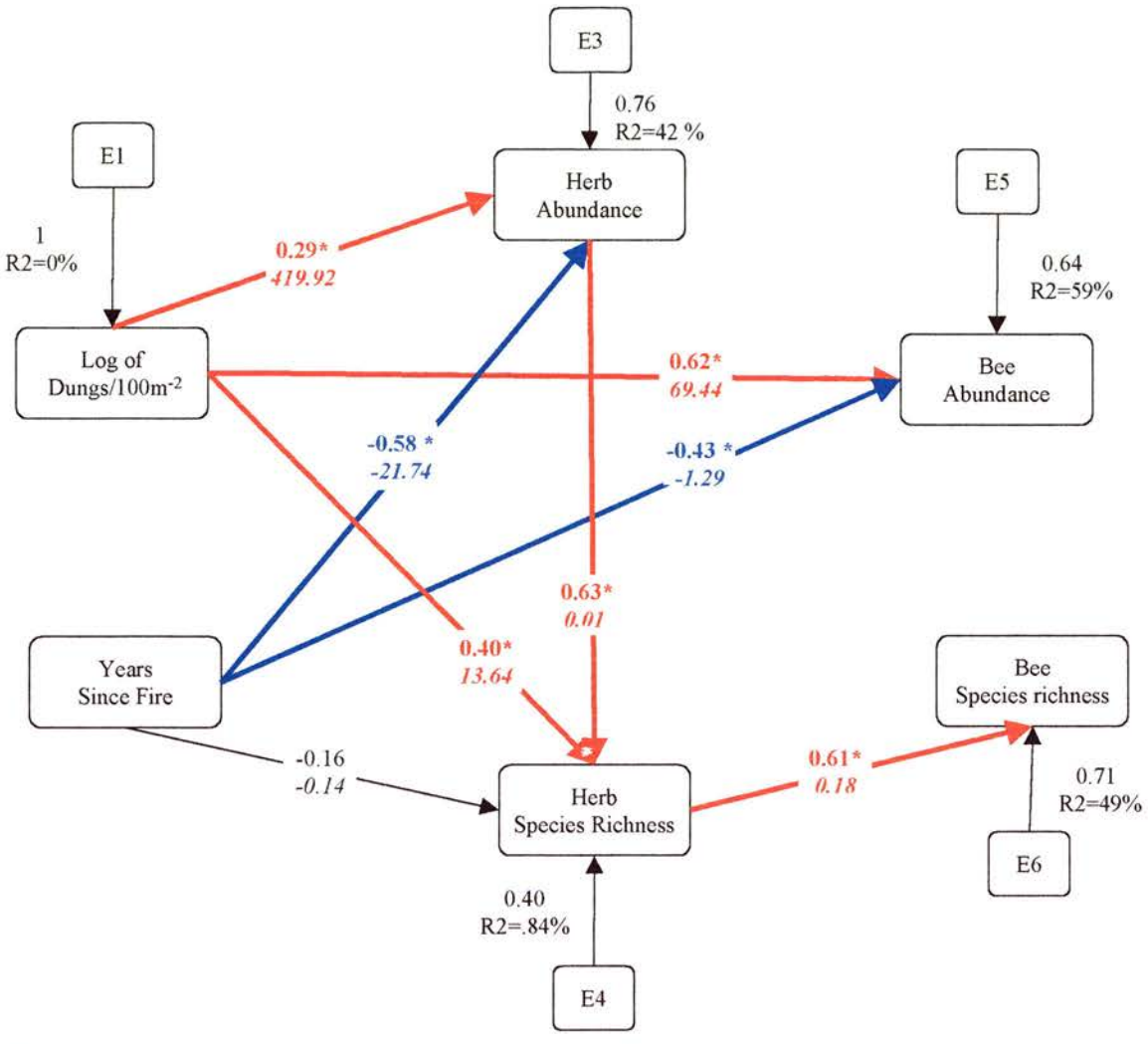


Figure 4.17 EQS model, looking at the paths explaining the abundance and species richness of bees. χ^2=5.93, P=0.31, CFI=0.99, RMSEA=0.08. Values are shown as in Figure 4.16 but non-standardised values are also given for partial regression coefficients. These are shown in italics.

Since it is unlikely that site age or grazing would directly affect bee abundance, this relationship must come about via some other route, which caused site age to have a negative effect and grazing to have a positive effect on bee abundance. The amount of bare ground, nectar energy and pollen grain number were all put in to the path model to try to explain this route, but the direct paths were always significant, whilst the others were not. It may be the availability of other nesting materials and sites, or the diversity of nectar niches (Potts *et al.* Unpublished manuscript), or the particular composition of flower communities, which are important. Another factor, which may

have a large effect on total bee abundance is the positioning of honeybee hives. It may be that the areas where farmers prefer to place their hives are more likely to be either recently burnt or highly grazed, and therefore more open. This would then fit in with the negative effects of site age and the positive effects of grazing intensity shown by this path diagram.

4.4.5 Summary of section 4.4

a) Year 1999	Dungs 100m^{-2}
Flower species richness	**<0.001**
Flower abundance	0.056
Bee species richness	0.871
Bee abundance	0.567

b) Year 2000	Dungs 100m^{-2}
Herb species richness	**<0.001**
Flower species richness	**<0.001**
Bee species richness	**<0.001**
Bee abundance	**<0.001**
Flower abundance in 17 yr old sites	**0.001**
Shrub abundance	**0.001**
Herb abundance	0.015
Shrub species richness	0.029
Flower abundance in 2 year old sites	0.085
Flower abundance	0.093

Table 4-2 Summary of the relationships between flowers and bees and grazing in a, 1999 and b, 2000. The numbers given are the P values. Those in Bold remain significant after SBA.

- Moderate grazing increases flower species richness, particularly of herb flowers, but intensive grazing decreases it again.
- This relationship is probably similar for bees but it is uncertain what is the optimum grazing level for bee species richness.
- The abundance of herb flowers increases with grazing intensity at all the levels surveyed, whereas the abundance of shrub flowers decreases.
- Bee abundance also increases with grazing intensity at the levels surveyed.
- All these effects are clearest in the 17 year old sites. This may be because the 17 year old sites had the highest grazing levels, or may be because grazing has

the most impact in intermediate aged sites.

- Path analysis shows that increasing post-burn age has negative effects on species richness and abundance of bees, whereas grazing has positive effects.
- The effects of both fire and grazing on bee species richness are effected via changes in the herb community. However the effects on bee abundance are caused by some other route which is not explained by herb abundance or species richness.

4.5 The effects of grazing on specific groups of bees

For this analysis data from year 2000 only were used, since these were the only data collected at high grazing levels. However, these data were only collected from mid March until late May and may therefore miss any species only present early in the season.

4.5.1 Abundance within families

When bees were split into families (Figure 4.18), numbers of Andrenidae, Megachilidae and Colletidae were consistently low so that no changes across grazing levels were obvious. Apidae appeared to increase slightly at intermediate grazing levels then decrease again, whereas halictid numbers kept increasing up to very high grazing levels.

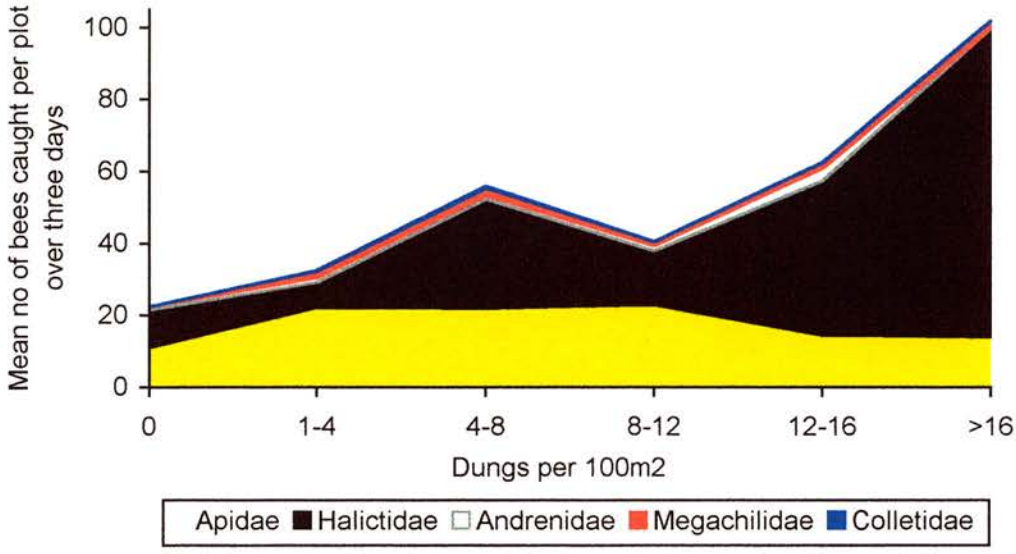


Figure 4.18 Proportion of bee catch made up of each family at different grazing levels.

When the numbers of Halictidae were adjusted for effects of fire, this increase with dung levels was found to be significant (SROC: r_S=0.418, n=30, P=0.021, Figure 4. 19). The number of Apidae did not change significantly (LR: R2=2.2%, n=30, P=0.134) with grazing intensity.

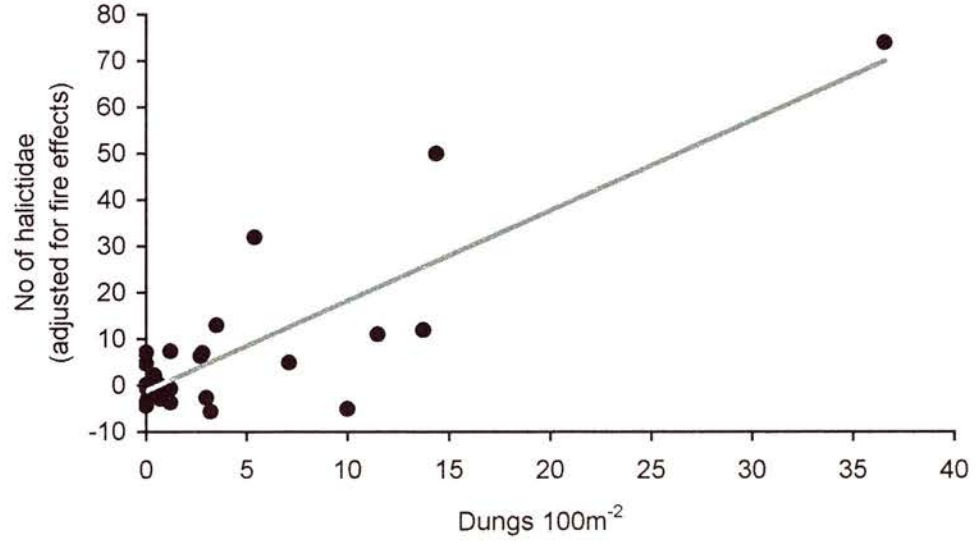


Figure 4.19 Number of Halictidae caught or identified, plotted against grazing intensity.

One possibility was that this change in numbers of Halictidae may be due to increased availability of areas of bare soil (used for nest sites) at higher grazing intensities. To look at the relationship between bare soil and dung levels, recently burnt sites were excluded since these already had large areas of bare soil caused by intensive burning. Areas of bare soil caused by tree shading were also excluded. The area of bare soil did then increase with grazing intensity (Figure 4.20, LR: R^2=43.9%, n=21, P<0.001).

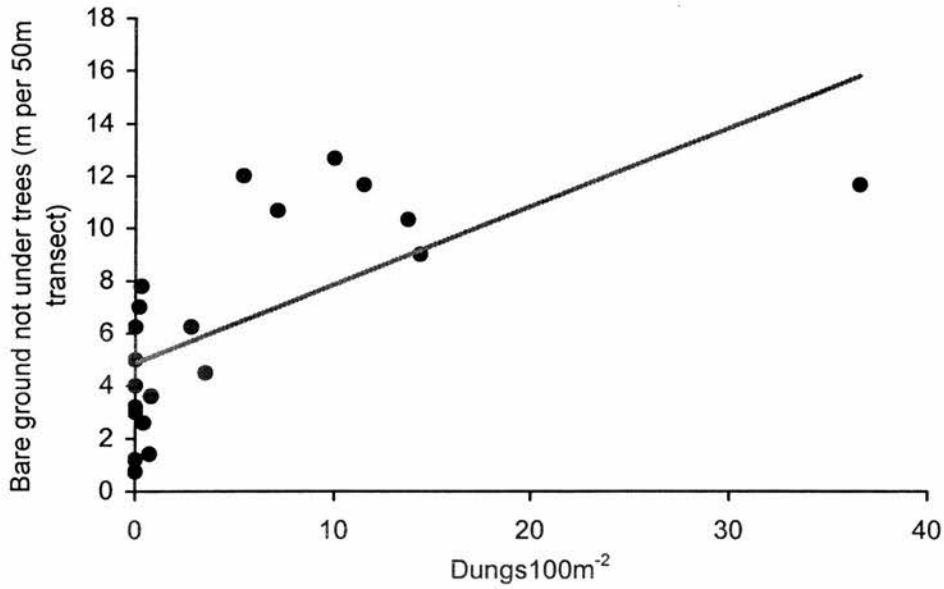


Figure 4.20 Area of bare ground related to grazing intensity.

However the abundance of halictids was not related to the availability of bare soil (SROC: r_S=-0.318, n=30, P=0.087) although the number of halictid species was positively related to the availability of bare soil (Figure 4.21; SROC: r_S=17.3%, n=30, P=0.049).

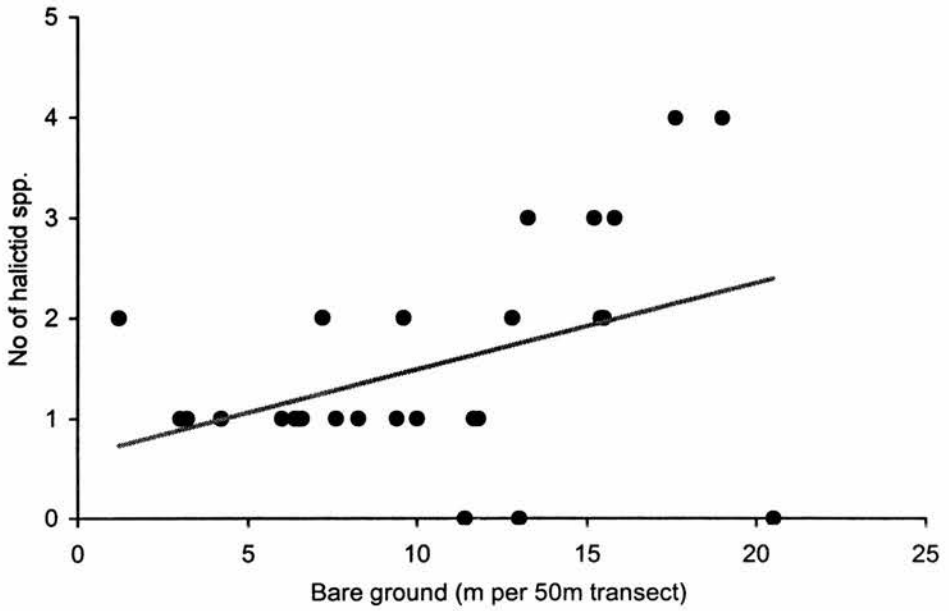


Figure 4.21 Halictid abundance related to the proportion of bare soil.

Halictid number was not significantly related to flower abundance (SROC: r_S=0.394, n=30, P=0.031, Critical P value after SBA =0.025), but did increase with the abundance of composites (Figure 4.22; SROC: r_S=0.552, n=30, P=0.002), on which these small bees were frequently seen feeding, both in this study and by Christopher O'Toole (pers. comm.). Since halictid abundance appears to increase more steeply at the lower end of the scale, and then level out, it may be that composite abundance is only limiting up to a point.

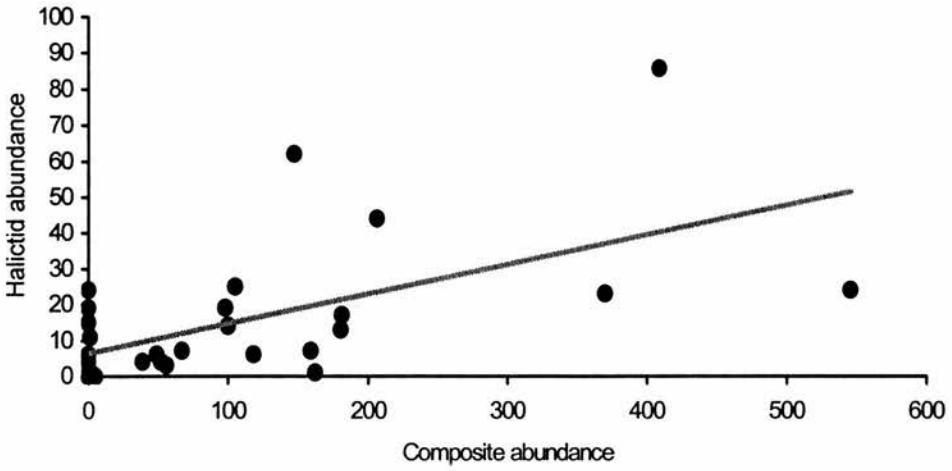


Figure 4.22 Halictid abundance related to composite abundance.

Composite abundance also increased at high grazing levels (Figure 4.23: SROC: r_S=0.886, n=30, P<0.001). Halictid numbers were not affected by the overall species richness of flowers (SROC: r_S=0.209, n=30, P=0.267) but increased with the species richness of composites (r_S=0.443, n=30, P=0.014).

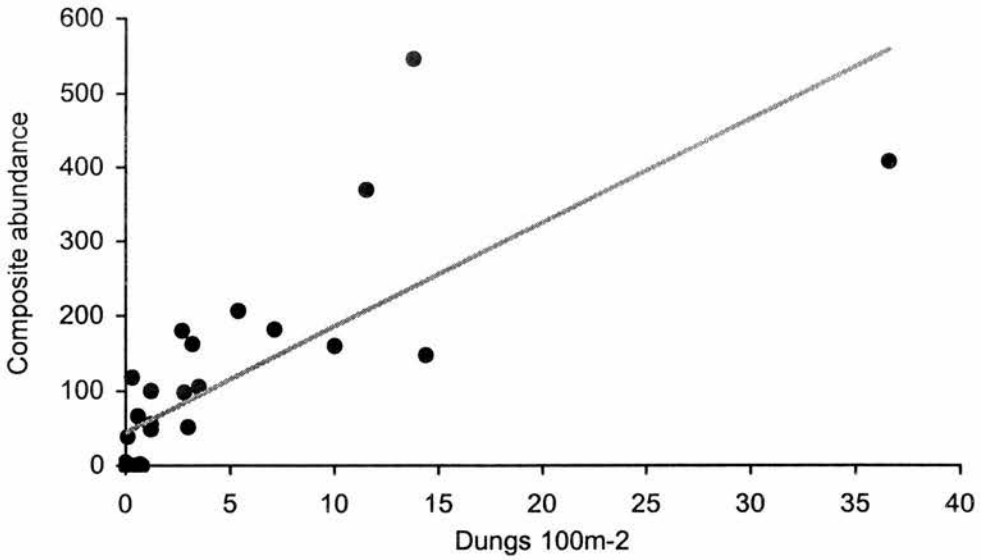


Figure 4.23 Composite abundance related to grazing level.

4.5.2 Species richness within families

The most speciose family at all grazing levels was the Apidae (Figure 4.24) which made up 44.4% of the 93 species.

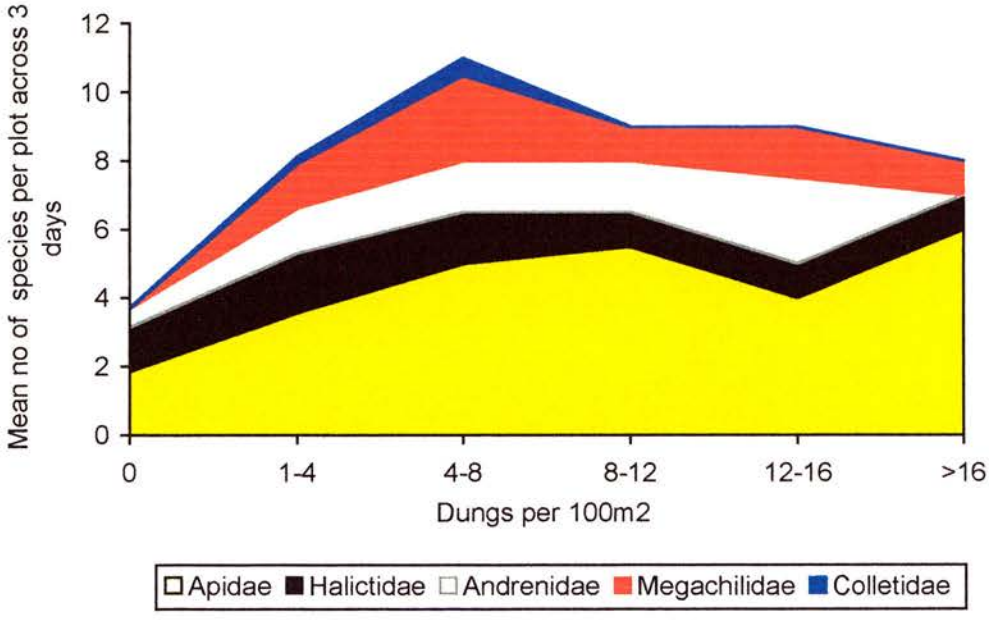


Figure 4.24 Species richness within families, plotted against grazing level.

The number of species in this family increased significantly with grazing intensity (SROC: r_S=0.581, n=30, P=0.001). The increasing species richness of Apidae with grazing levels (Figure 4.25) was probably explained by the increase in flower abundance (SROC: r_S=0.490, n=30, P=0.006) and flower species richness (LR: R^2=42.2%, n=30, P<0.001).

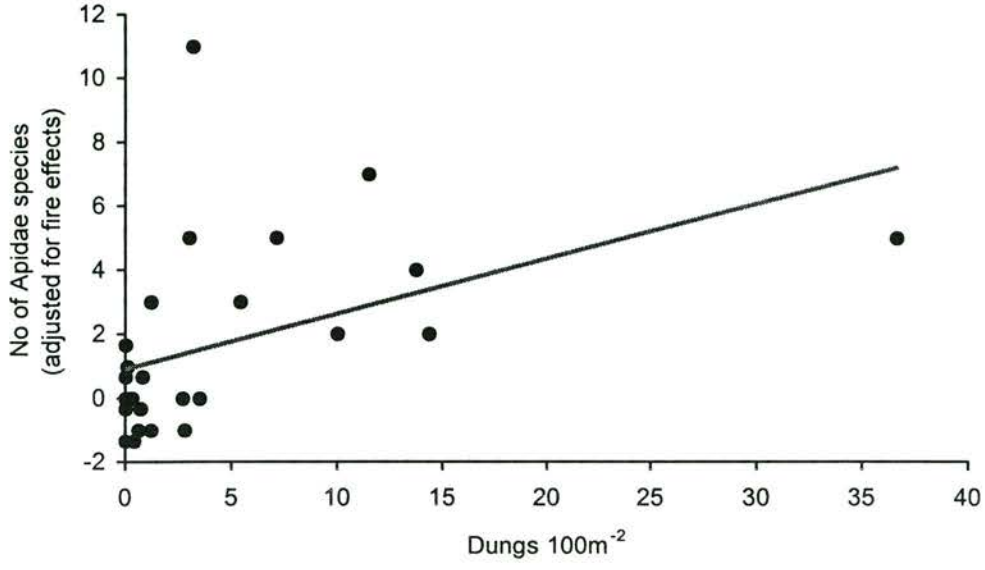


Figure 4.25 The relationship between apid species richness and grazing intensity.

Species numbers in the other families were not high enough to show any definite changes but the number of halictid species was relatively constant and both the Andrenidae and the Megachilidae had most species at intermediate grazing levels.

Summary of sections 4.5.1 and 4.5.2.

The table below shows those relationships included in Sequential Bonferroni Adjustments for sections 4.5.1 and 4.5.2

	Dungs/100m-2
Bare soil	**0**
Composite abundance	**0**
Apid species richness	**0.001**
Halictid abundance	**0.021**
Apid abundance	>0.05

	Halictid abundance
Composite abundance	**0.002**
Composite species richness	0.014
Flower abundance	0.031
Flower species richness	0.267
Bare soil	0.087

Table 4.3 Summary of the relationships with grazing levels and with Halictid abundance, looked at in section 4.5.1 and 4.5.2. Numbers are P values. Those in Bold are still significant after SBA.

4.5.3 Dominant bee species.

A total of 1051 bees were identified for the last 3 rounds in year 2000, including 93 species. However the majority of individuals were of the same few species as can be seen from Figure 4.26.

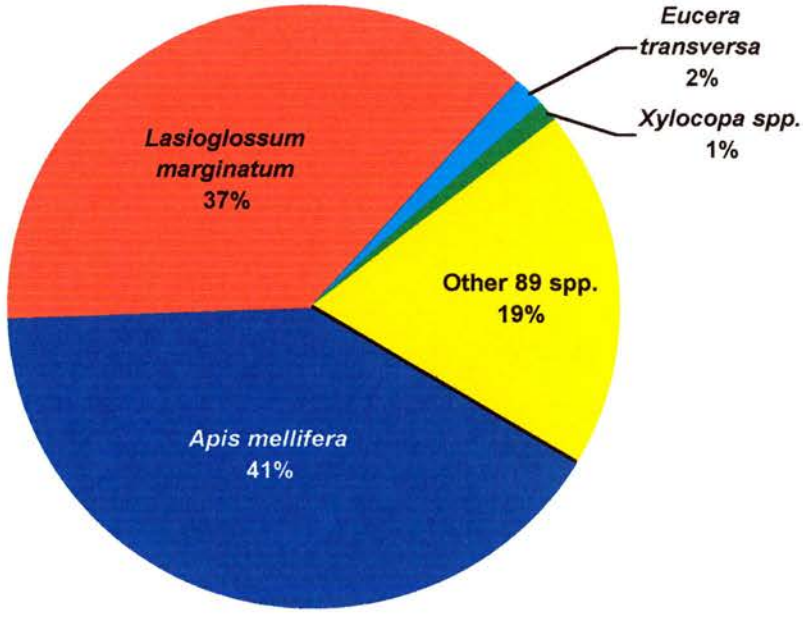


Figure 4.26 Abundance of bees of each species as a percentage of the total bee abundance.

Those bee species which made up at least one percent of the total were looked at in relation to grazing. These were *Apis mellifera* 41%, *Lasioglossum marginatum* 37%, *Xylocopa* 1.05%, and *Eucera transversa* 1.8%. *Apis mellifera* and *Lasiglossum marginatum* may be slightly over-represented since these were identified when sitting on flowers or in flight as well as being caught.

Apis mellifera was not significantly affected by grazing levels and neither were *Xylocopa sp* or *Eucera transversa* (all P>0.05). Numbers of *Lasioglossum marginatum* did increase with grazing intensity, but not quite significantly (Figure 4.27, SROC: r_S=0.370, n=30, P=0.044, Critical P-value after SBA =0.013).

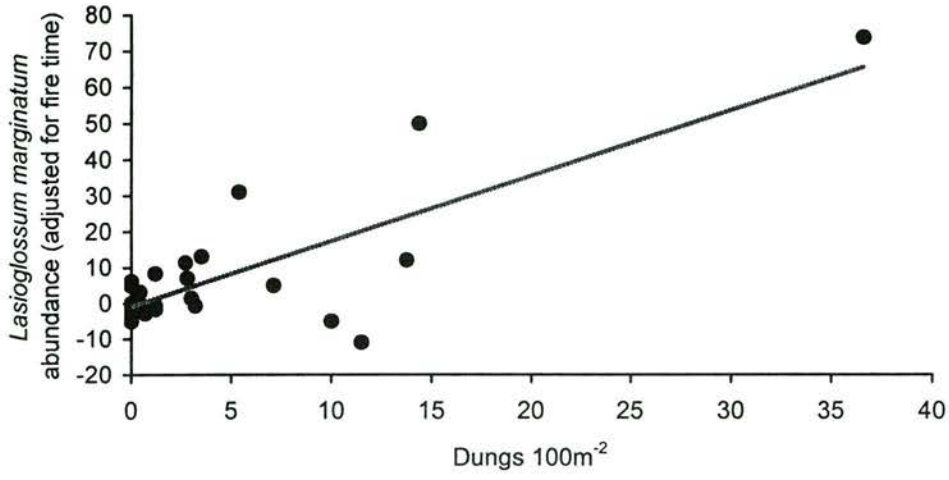


Figure 4.27 Abundance of *Lasioglossum marginatum* with increasing grazing intensity.

This trend is not surprising since *L. marginatum* made up 92.6 % of all the halictids which themselves increased at high grazing levels (Figure 4.19). As was found for the halictids overall, the numbers of *Lasioglossum marginatum* were significantly related to the abundance of composites (r_S=0.403, n=30, P=0.027).

Since the number of halictids increased with grazing and was limited by the abundance of composites, it could be that composite abundance would explain the relationship between grazing and bee abundance, described in section 4.4.4. When composite abundance and halictid abundance were put into the path model a reasonable fit was obtained since P was greater than 0.05, χ^2 was low (4.33) and CFI was close to 1 (though RMSEA was slightly higher than it should be). This model still showed that the effects of grazing and fire on bee abundance were not via composite abundance, but it did show that grazing increased bee abundance by increasing the number of halictids (Figure 4.28).

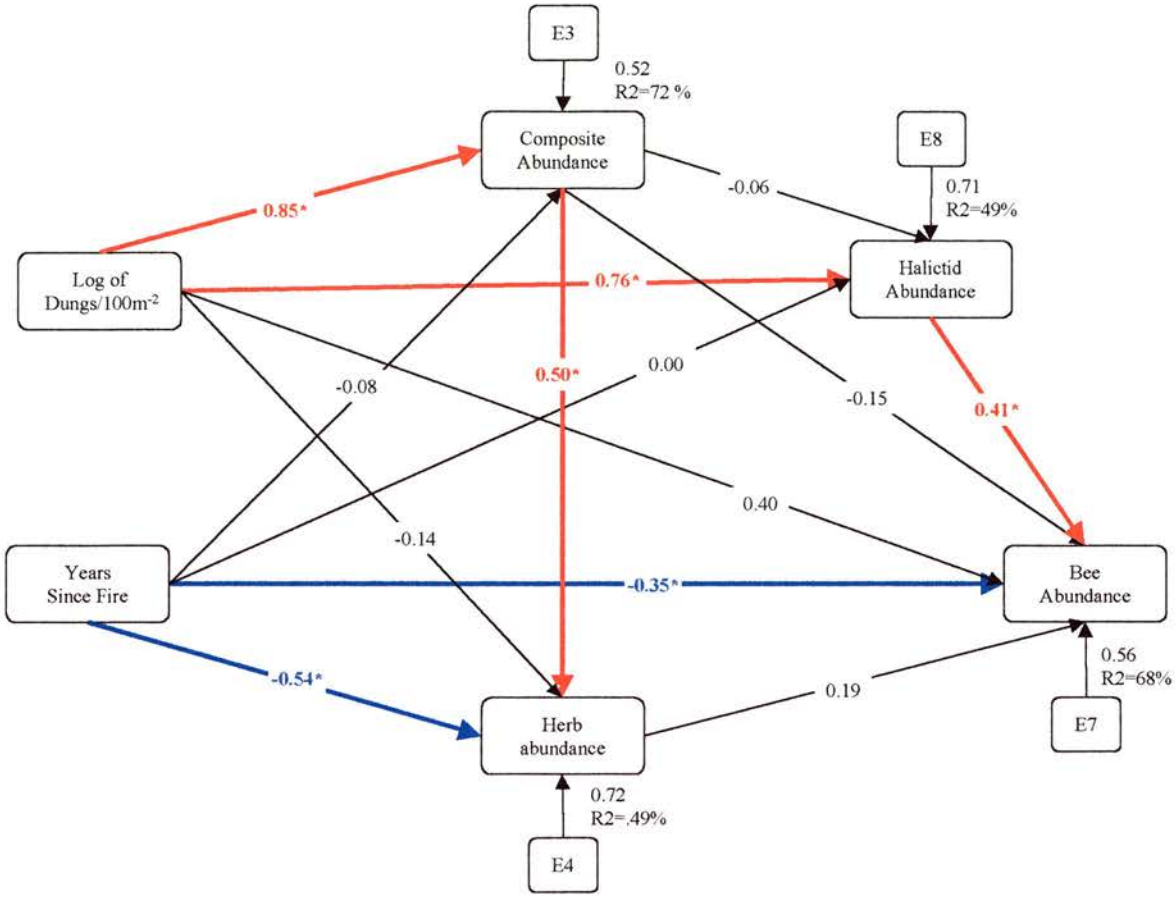


Figure 4.28 EQS model, looking at the paths explaining The abundance of bees. χ^2=4.33, P=0.11, CFI=0.98, RMSEA=0.20. Values on diagram are partial regression coefficients. Those in blue show negative relationships and those in red show positive ones. Bold coloured lines show significant relationships and narrow black lines show insignificant ones.

4.5.5 Summary of section 4.5

- Halictid numbers increased with grazing intensity and this correlated with the increase in composite abundance at higher grazing levels. Over 90 % of the Halictidae were *Lasioglossum marginatum* which also increased with grazing and with composites.
- The increased abundance of bees at high grazing levels was related to the changes in halictid abundance, but not to changes in composite abundance.
- The species richness of Apidae increased at high grazing intensity, which was

related to the increase in flower abundance and species richness with grazing.

4.6 Discussion

4.6.1 Flowers

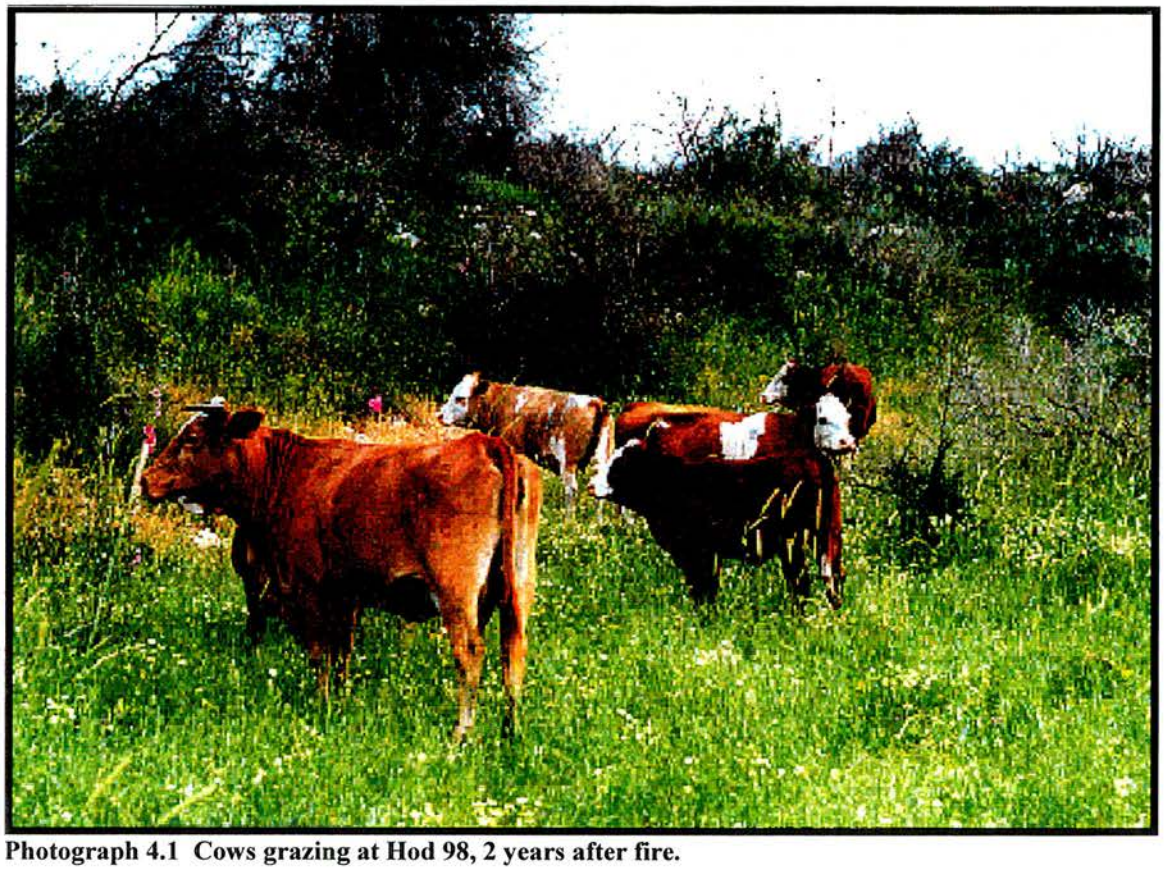
Flower diversity increased with grazing intensity in 1999 but none of the sites surveyed in the first season were heavily enough grazed for diversity to be reduced again, as predicted by the intermediate disturbance hypothesis (Connell 1978). Nor was grazing heavy enough to have any clear effect on the abundance of flowers. In the second field season however, when a more complete range of grazing levels was examined, flower species richness did fit the intermediate disturbance hypothesis, reaching a maximum at around 100 dung pats 100 m^{-2} then decreasing again.

The variation in flower species richness in this study was caused mainly by changes in the composition of herb species, whereas the number of shrub flower species was reduced slightly (though not significantly) by grazing. However, their actual cover (the amount of ground they covered) must have been decreased by grazers more than was measured in terms of flowers which would leave space for the smaller, light-demanding annuals. This was similar to patterns seen previously in *Quercus calliprinos* woodland in Israel (Naveh and Whittaker 1979a) where the species richness of annual and perennial herbs was highest at moderate to heavy grazing levels, whereas the dominance of the woody strata was limited by grazing.

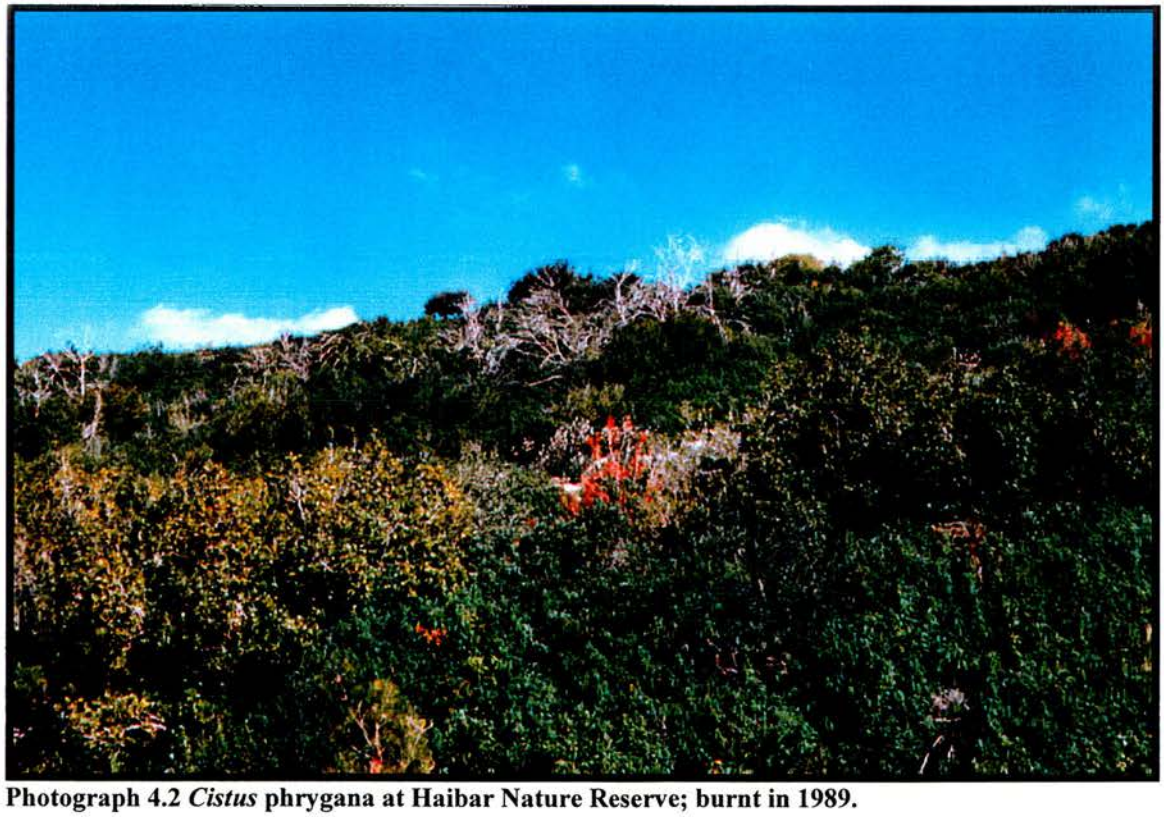
Although flower diversity was highest at intermediate grazing levels, the abundance of herb flowers simply increased with grazing intensity, even at the highest levels. Conversely, the abundance of shrub flowers decreased at high grazing levels, so that

when herbs and shrubs were combined there was only a slight increase in flower abundance overall, and only in the 17 year old sites. Since annuals are mainly herbs, this agrees with Cornelius *et al.* (1997) and Milchunas *et al.* (1993) who found that grazing increased annual cover, and with Petanidou and Ellis (1996) and Naveh (1982) who discovered that a lack of grazing in phrygana resulted in an homogenous layer of shrubs.

These effects were only obvious in the intermediate aged sites, partly because it was only in the Mitla area (Mit83 MitShed and MitBot) that grazing levels were relatively high. However grazing probably did have different effects in sites of other ages. The main effect of grazing is to remove or handicap the dominant species (Ellison 1960; Smith & Smith 2001), which in this case are the dominant shrubs, allowing less competitive species to grow. In recently burnt sites, however, flowers were extremely abundant and diverse even without grazing, and though most of the shrub species were already present, they had not yet become large enough to shade out the herbs. This meant that no species was yet dominant. The presence of grazers in these sites (Photograph 4.1) could therefore make less difference than in the intermediate aged sites, where when grazers were absent shrubs such as *Cistus spp.* and *Calycotoma villosa* formed a uniform layer (Photograph 4.2).



Photograph 4.1 Cows grazing at Hod 98, 2 years after fire.



Photograph 4.2 *Cistus* phrygana at Haibar Nature Reserve; burnt in 1989.

The intermediate aged sites at Mitla (burnt in 1983) have been grazed by cattle since about 6 years after they were burnt. Grazing may therefore have slowed down the growth of the shrubs and kept the contribution of annuals high since then, as was found by Perevolotsky *et al.* (1995) who used cattle to keep fire breaks open in Israel. Since grazing is known to improve the palatability of some plants (Wallis DeVries 1996), it is also likely that cattle have returned repeatedly to previously grazed patches of young, palatable growth and therefore maintained patches of herbs, amongst stands of shrubs. This will be discussed further in Chapter 5.

There was virtually no sign of grazing at all in any of the sites over 26 years old, and the long term grazing histories in these areas were not ascertained, real information is not available on the impact of grazing in mature forests. However, the dominant species in the mature areas was *Pinus halipensis*, which could not have been affected by grazing once above a certain size. Even so, young trees may be disturbed by trampling, so in areas grazed over long periods the distribution of trees might have been altered if they were grazed as seedlings. Although the cover of shrubs was lower in the oldest sites, the understorey was generally made up of the same shrub species that formed the dominant vegetation in younger sites. I would therefore expect grazing to have similar effects to those seen in intermediate aged sites. However, due to shading by trees, the abundance of both shrubs and annuals will always be lower than in younger sites.

4.6.2 Bees

The relationship between grazing and the species richness of bees was less clear than between bee species richness and flowers. In general it seems that the grazing has a

positive effect on the species richness of bees; yet at the site with most grazing pressure (Shed 2), species richness was not as high as might be expected if grazing effects were entirely beneficial to bees. Although bee species richness might decrease further at even higher grazing levels, from the available data it is not certain where the optimal grazing level lies. Bee abundance, on the other hand, increased steeply with grazing levels, though once again this pattern was only clear for the intermediately grazed sites.

4.6.3 Flowers and Bees

The sites surveyed had high enough grazing levels to cause a decrease in diversity of flowers, but not to cause any decrease in abundance. As predicted in Section 1.5.3, flower and bee abundance must be reduced by grazing at some point but not at the levels of grazing measured in this study. This was seen for flowers, in one part of Shed 2 (described in Section 4.2.3 a), though the area without flowers was small so bees still flew over it. The abundance of both bees and flowers was greatest at high grazing levels, when flower species richness had already decreased, leaving only those species best-adapted to grazing.

Since all measurements were taken across the whole season, temporal effects may have been concealed in this analysis. The flower species present in the very highly grazed sites were mainly nitrophiles such as *Malva* spp, *Silybum marianum* and *Chrysanthemum coronarium*. These plants had a very fast burst of growth and flowering in the middle of the season, so attracted a large number of bees at this time, but then died completely leaving little else (Photograph 4.3). If the start and end of the season were looked at separately, I would expect the abundance of both bees and

flowers to be much lower in the most highly grazed sites, in which case we would see a unimodal relationship with grazing in some parts of the season.

Photograph 4.3 An intensively grazed area at Shed 2 in early May 2000.

The main changes in the bee community due to both grazing and fire were expected to take place via changes in the floral community. Path analysis showed that as far as species richness was concerned this was true. Neither fire nor grazing had direct effects on the diversity of bees. Fire did have a negative effect on the species richness of herb flowers, and grazing (when log transformed to account for the curved relationship) had a positive effect. The species richness of herb flowers was in turn positively related to the species richness of bees. When looking at bee abundance however, the relationships were not as expected. Both herb flower abundance and bee abundance increased with increasing grazing intensity and decreased with time since fire, yet it seems that the changes in bee abundance were not caused by the changes in

herb abundance. Other possible factors which may have caused fire to have negative effects and grazing to have positive effects on the abundance of bees were the availability of bare ground for nesting, nectar energy or pollen grain number. However none of these fitted the path model. The relationships could alternatively be explained by some other route, such as the availability of other nesting sites and materials or the particular composition of flower communities.

Since 78% of all bees were either *Apis mellifera* or *Lasioglossum marginatum*, factors affecting these two species probably determine the overall abundance of bees. The position of beehives could be important since 41% of all bees seen were *Apis mellifera,* yet *A. mellifera* abundance was not related to grazing levels. The only bee group which seemed to be affected specifically by grazing was the Halictidae, which made up 40.7% of all bees, and of which the majority (92.6%) were *Lasioglossum marginatum*. According to path analysis, the increase in bee abundance at high grazing levels was explained by the increased number of Halictidae, but halictid numbers were not affected by the time since burning. Composite abundance was correlated with halictid abundance, but path analysis suggested that the increase in numbers of Halictidae due to grazing was not explained by the abundance of composites. However *L. marginatum* is known to have a preference for composites, (O'Toole, pers. comm.) and so it **may** be a particular group of composites or else the amount of nectar and pollen available from composites, which is limiting. Since it was not possible to measure nectar production by composites, further work would be needed to test this.

There may also be other factors affecting the distribution of these bees.

L.marginatum, are primitively eusocial, and have colonies often exceeding 200 bees (O'Toole & Raw 1991). It is not known how far individuals of this species are able to travel but they probably do not go more than 300m from the nest (O'Toole, pers com) and so the high abundance at all 3 Mitla sites is likely to be due to a number of nests in each plot. Although path analysis showed the abundance of these bees was not related to the availability of bare ground, it is known that they nest in disturbed and slightly compacted earth (O'Toole, pers. comm.) so it may be a combination of the hardness of the ground and the availability of open areas which limits their abundance.

Overall, bee species richness is positively affected by grazing, and this is mainly due to increased flower species richness. Bee abundance also increases with grazing levels and, though it must decrease again at some point, this must happen at much higher grazing levels than were included in this survey. The abundance of bees is affected by grazing, mainly due to increased abundance of halictids, and this **may** be related to the availability of rewards from composites (which it was not possible to measure) and of suitable nest sites in disturbed and compacted ground.

5 Grazing and vegetation structure

5.1 Introduction

As well as changing the diversity and abundance of flora, trampling and defoliation by grazing animals alters vegetation structure. The most obvious effect of defoliation is a reduction in the height of vegetation. However it was suggested by Grubb (1976) and Grime (1979) that, in chalk grasslands, grazing opens up gaps within a heterogeneous sward, rather than simply reducing the height of all the vegetation. This has been found for various grassland habitats, including Mediterranean grasslands in Israel (Noy-Meir *et al.* 1989), tall-grass prairie in Oklahoma and Kansas (Collins 1987; Damahoureyeh & Hartnett 1997, respectively), and upland grasslands in Scotland (Dennis *et* al 1998). Since grazing increases the availability of palatable new shoots, cattle repeatedly return to the same areas and this patchy structure is maintained (Gibb and Rideout 1986, 1988; Wallis DeVries 1996).

Similar effects have also been seen in phrygana; in both Israel (Naveh 1982) and Greece (Petanidou & Ellis 1996), a lack of grazing resulted in a monotonous shrub layer with few open patches, whilst on the SE Iberian Peninsula grazing by sheep and goats created a mosaic of grassland and shrubland (Verdu *et al.* 2000). However these changes have not been specifically measured, as they have in grasslands. In phrygana habitats, the dominant species are woody shrubs, therefore in order to create open patches grazers must inhibit the growth of these woody species and encourage the growth of annuals, as cattle were found to do in Israel (Perevolotsky *et al.*1995). Since cattle tend to avoid feeding on woody species except when there is no other option (Seligman & Gutman 1979; Noy-meir *et al.* 1989), it may be that open patches

are only created at relatively high levels of grazing. However at lower grazing levels the growth of shrubs may be inhibited by defoliation when they are still seedlings. Larger shrubs may also be broken by trampling as cattle push through them. Either way, the production of herbs is likely to increase wherever shrubs have been removed, so that once open areas have been formed, cattle will continue to graze the same patches and keep them open.

As discussed in Chapter 1, both shrub patches and open areas are likely to be important in maintaining a diverse community of bees. Many species of bees require open areas, with a high abundance of annual flowers and areas of bare ground for nesting. However some also need areas of scrub, which provide woody plants with cavities for nesting, and perennial plants with high nectar rewards. A habitat with heterogeneous vegetation is likely to provide the variety of microclimates needed by different species (Willmer 1982). However woody plants may also provide shelter for predators such as birds (Soderstrom *et al.* 2001) and spiders (Gibson *et al.* 1992a). The optimum "patchiness" for bees is therefore likely to occur at intermediate grazing levels, where there is adequate bare ground for nesting and annual plants are abundant and yet enough shrubs are still present to provide adequate nesting sites and shelter.

It was shown in Chapter 3 that bee communities were limited mainly by the abundance and species richness of herb flowers, so it is likely that an increase in the area of open patches will affect the rewards available to bees mainly by increasing the availability of herb flowers. Herbs will benefit from the removal of shrubs due to decreased competition for light and nutrients. However if not all of the shrubs are removed, those which remain may also benefit from this decreased competition.

The variety and density of organisms is often greatest around habitat edges (Smith and Smith 2001) since many species benefit from the diversity of environmental conditions within these boundaries. As shown by Damahoureyeh & Hartnett (1997), forbs which are not grazed may have increased growth and fecundity when the dominant species surrounding them are removed due to the increased availability of light. Those shrubs at the edges of open patches may then be able to produce more flowers than those surrounded by other plants. This was shown for *Eupatorium rugosum* (Asteraceae) in Virginia (Landenburger & Ostergren 2001). The abundance of flowers declined with increasing distance from the edges of cleared areas of forest. This was due partly to light availability, but also to changes in other environmental factors which were not measured.

As well as producing more flowers, shrubs at the edges of patches may also be able to benefit from increased light and nutrients such that they produce superior nectar and pollen rewards within each flower and may be more visible, therefore attracting more pollinators. Hence the number of open patches may be important to bees because of changes in rewards provided by the shrubs at the edges of patches as well as changes in the diversity and abundance of annual flowers.

In this Chapter the way in which grazing affects the structure of the vegetation in Israel and the way changes in vegetation structure affect the diversity and abundance of flowers and bees were investigated. There was then a more detailed investigation of some areas of patchy vegetation in Lesvos (Greece), to find out whether reward production by two of the dominant shrubs (*Lavandula stoechas* and *Cistus creticus*) differs between plants at the edges of open patches and those surrounded by other

shrubs, and what effects this has on the pollinators visiting them. This will help to show whether the effects of grazing on bees are simply due to increased abundance and diversity of herb flowers in open patches, or whether they are also affected by changes in the rewards produced by shrub species.

5.2 The effects of cattle grazing on vegetation structure.

This section uses data from 3 rounds in year 2000 only, as vegetation height was only measured in detail during the second field season. Data are adjusted to account for the effects of fire, as in Chapter 4 (Section 4.2.1). Vegetation height was measured to the nearest 5cm, at points every 1m along 50m transects. If more than one stem touched any point on the tape, then the tallest was measured.

Grazing was found to decrease the overall height of vegetation in 2000 (LR: R^2=44%, n=30, P<0.001) as in Figure 5.1 (a). However the main effect seemed to be in the intermediate aged sites. As can be seen from Figure 5.1 (b) the other sites were not affected. This may have been partly due to the low grazing levels in these other sites, but was also probably due to the fact that the other moderately grazed sites were, coincidentally, recently burnt, and therefore vegetation height was already low and could not be greatly altered by grazing.

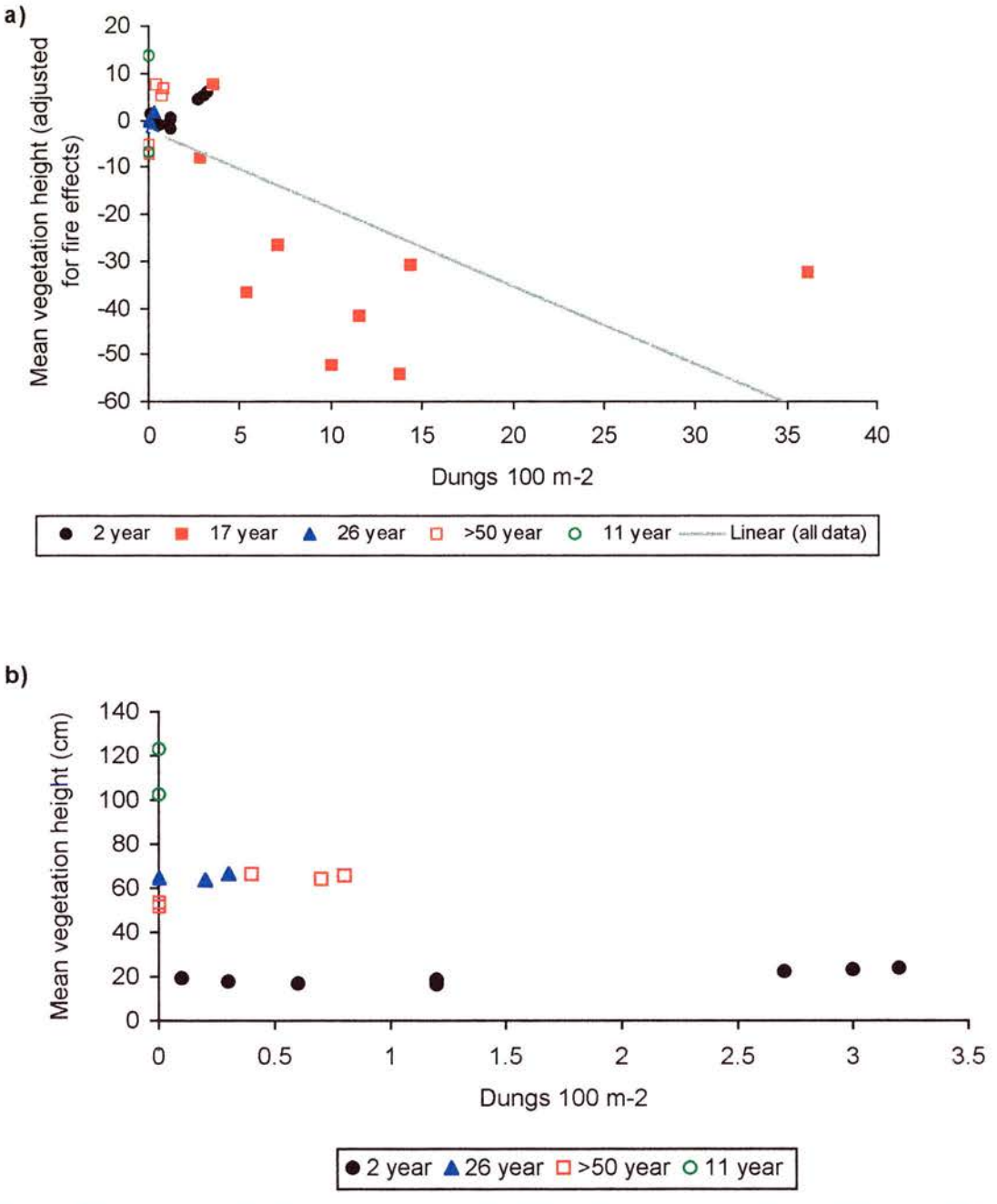
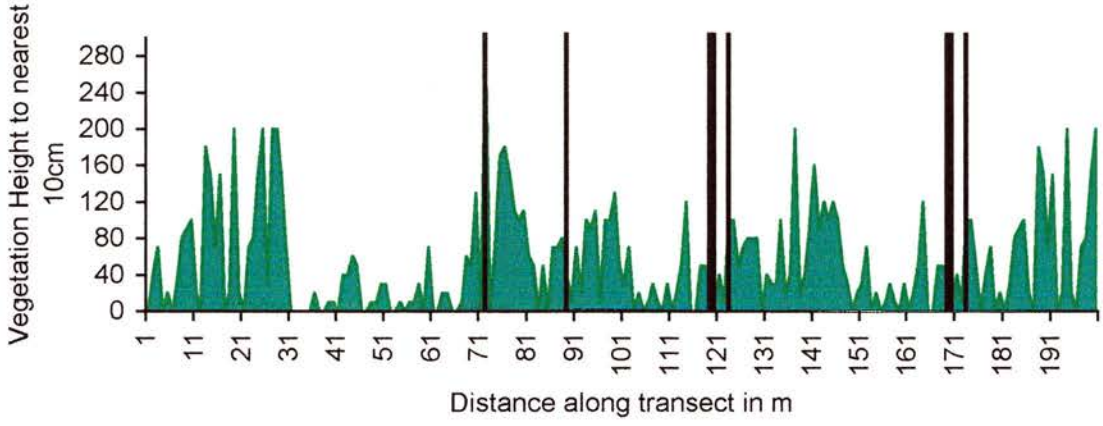


Figure 5.1 The relationship between vegetation height and grazing in 2000 (a) All sites. (b) All except 17 year old sites.

Although the mean height of vegetation in the intermediate aged sites was decreased by grazing, the range of heights stayed similar, as can be seen from Figure 5.2. This shows examples of cross sections from (a) a moderately grazed site, burnt in 1983, and (b) a protected site burnt in 1989. Rather than decreasing the height of all the

vegetation, grazers opened up (or kept open) gaps within what would otherwise be a continuous stand of shrubs, therefore increasing the variation in vegetation heights.

a) Grazed, 17 years since fire.



b) Ungrazed. 11 years since fire

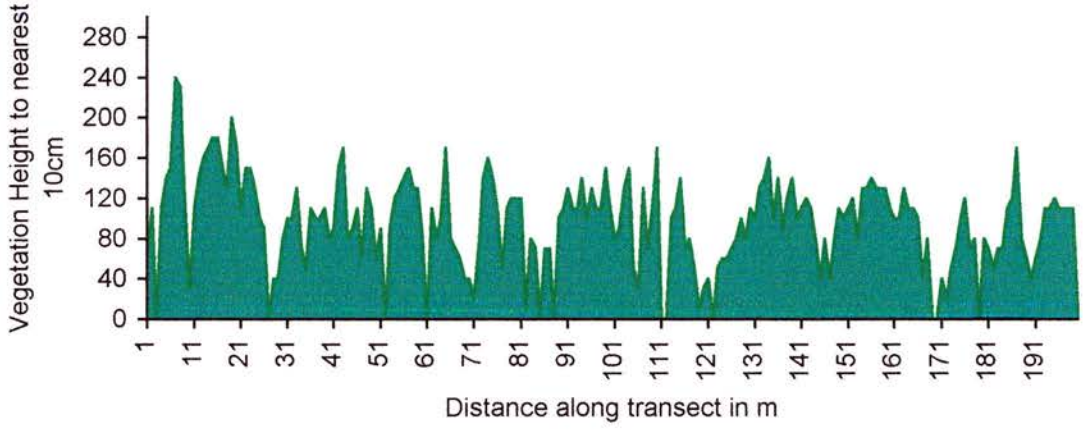


Figure 5.2 Cross sections showing vegetation heights at (a) "Mitla 3"burnt in 1983, with moderate grazing levels and (b) "Haibar 1" which burnt in 1989 and was completely protected from grazing. Black lines represent areas shaded by trees and green areas show all other vegetation.

5.2.1 Grazing and "patchiness".

To investigate this opening up of the vegetation, the "patchiness" of each site was measured. However the open areas did not have distinct edges so it was difficult to define what was a "patch" and what was not. It was necessary to decide which were

the main heights of vegetation represented in the type of open patch created by grazers. In order to do this, vegetation heights were categorised as 0, <10cm, <20cm, <30cm etc, up to <100cm. A series of Spearman's rank order correlations was done (Table 5.1), to discover whether the proportion of vegetation in any of these height categories was increased by grazing. Data from 17 year old sites only were used, in order to avoid confusion with the effects of site age.

Vegetation height (cm)	0	<10	<20	<30	<40	<50	<60	<70	<80	<90	<100
r_S	0.303	**0.678**	**0.700**	0.583	0.583	0.510	0.583	0.467	0.500	0.485	0.476
P	0.429	**0.045**	**0.036**	0.099	0.099	0.16	0.099	0.205	0.17	0.185	0.205

Table 5-1 Spearman's rank order correlations relating the heights of vegetation in 17 year old sites (m per 50m transect) to grazing levels (dungs 100m^{-2}). All n=9.

After Sequential Bonferroni Adjustments (Rice, 1989), only P<0.0045 should be strictly taken as significant. However the proportions of vegetation under 10cm high, and under 20cm high, were closest to being significantly correlated with grazing intensity. Since vegetation was only measured to the nearest 10 cm, there was very little difference between the <10 and <20 cm categories therefore these could both be combined in a <20 cm category (Figure 5.3).

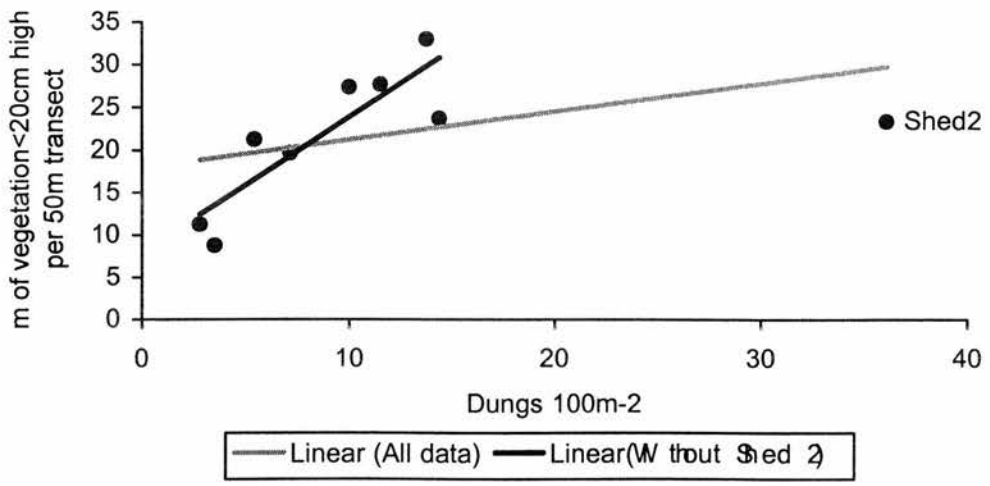


Figure 5.3 Proportion of vegetation < 20cm high, related to grazing levels.

The most intensively grazed site (Shed 2,) might have been expected to have a greater proportion of short vegetation than it did have. However a small part of Shed 2 had very high levels of dung and little vegetation except for thistles and nettles (as in Chapter 4, Photograph 4.3). This means that the mean dung level for the whole plot was very high, even though grazing was really only this intense in a small area of it. The vegetation in all but this small area was similar to that in the neighbouring plots. If Shed 2 was excluded, the relationship between grazing level and the amount of vegetation under 20cm high was significant (SROC: r_S=0.864, n=8, P=0.006), therefore this was the height used in this study to define open areas of vegetation.

The total area of patch, the number of patches and the mean size of a patch were calculated, including everything 20cm high or less as "patch" and everything over this height as "non-patch". Hereafter, the total proportion of vegetation under 20 cm high along any 50m transect is referred to as "**patch area**". "**Patch size**" refers to the mean diameter of patches of vegetation under 20 cm high and "**patch number**" is the number of individual patches of vegetation under 20cm high on any 50m transect. Areas of short vegetation under trees were assumed to be caused by tree shading rather than by grazing animals. Those areas of "patch" where there were trees directly above were therefore excluded when looking at the effects of grazing. Freshly burnt sites were also excluded from this analysis since the vegetation in these sites was almost all under 20cm high and so the patch area could not be increased by cattle.

Without including the freshly burnt sites, site age had very little effect on either the total area of patch, the number of patches or the mean size of patches (in the sites with < 1 dung $100m^{-2}$). Adjustment for fire effects, therefore, made no difference to the

relationships between these variables and grazing levels. Hence, further analysis was done, including all the sites except the fresh burns, without adjusting for fire effects.

5.2.1 a) Patch area (m of patch per 50m tramsect)

On this basis, the area of "patch" increased significantly with increasing grazing levels (Figure 5.4, line A, R^2=49.1%, n=21, P<0.001). If Shed 2 was excluded, then dung level (grazing) explained 77.5% of the variation in patch area (Figure 5.4, line B, n=20, P<0.001). From the data shown it seems likely that the area of patch increases up to about 50-60% of the total area (i.e. 25-30 m patch/ 50m transect), and then levels out somewhat or increases less steeply.

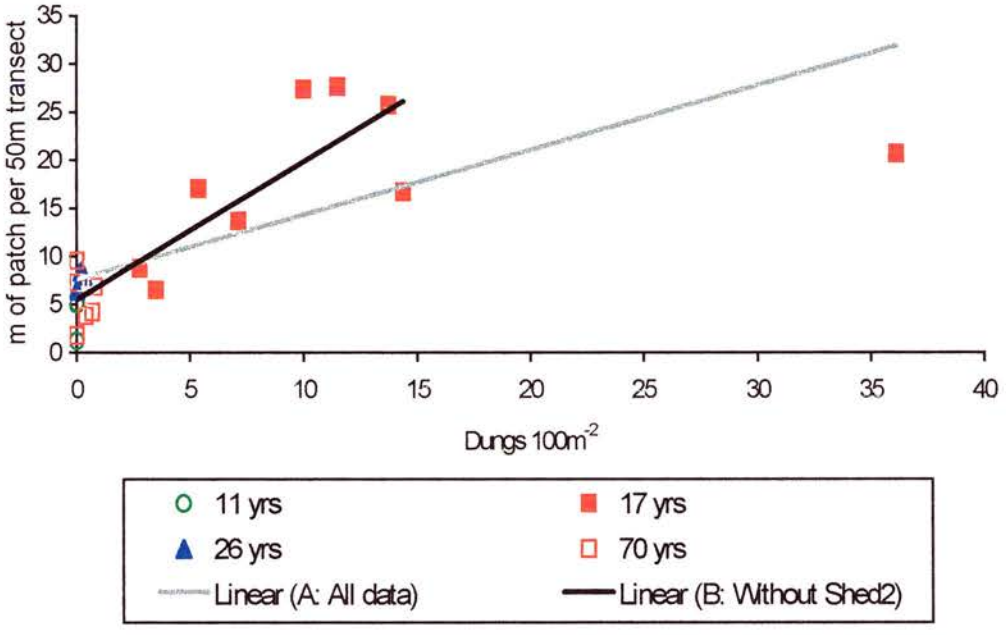


Figure 5.4 The relationship between grazing levels and the total area of vegetation under 20cm high.

5.2.1 b) Patch size (mean diameter of patches along a 50m transect)

Mean patch size also increased significantly with grazing levels (LR: R^2=82.5%, n=21, P<0.001) as shown in Figure 5.5. This was significant even when Shed 2 was removed (LR: R^2=56.6%, n=20, P<0.001).

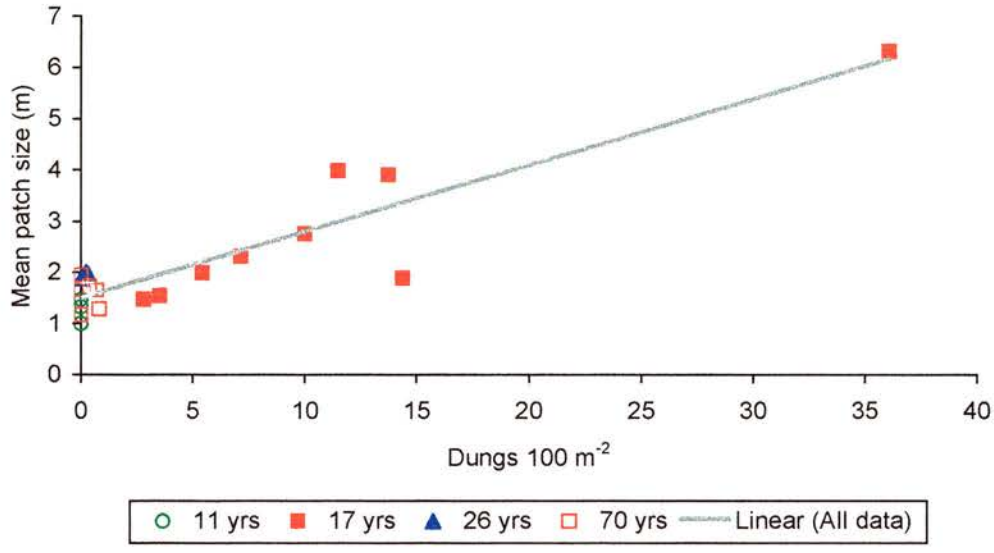


Figure 5.5 The relationship between grazing levels and patch size.

5.2.1 c) Patch number (mean number of patches along a 50 m transect)

The number of patches significantly fitted a polynomial curve (Figure 5.6, PR: R^2=68.6%, n=21, P<0.001), increasing with grazing intensity to start with but then decreasing again at high grazing levels. This curve fitted better than a straight line (FTEST: F=28.72, DF=1,18, P<0.0001), an exponential curve (FTEST: F=43.01, DF=1,18, P<0.0001) or a rectangular hyperbola (FTEST: F=40.9, DF=1,18, P<0.0001). The fit was still just significant even when Shed 2 was removed (PR: R^2=71.9%, n=20, P=0.040). This is because as patches get larger they will eventually join together, decreasing the total number of patches. Thus, as shown in Figure 5.7, patch number also has a unimodal relationship with patch size (R^2=42.8%, n=21, P=0.006). The data again fitted a polynomial curve significantly better than a straight line (FTEST: F=9.68, DF=1,18, P=0.006), an exponential curve (FTEST: F=4.831, DF=1,18, P<0.0412) or a one-site binding hyperbola (FTEST: F=5.83, DF=1,18, P=0.0266).

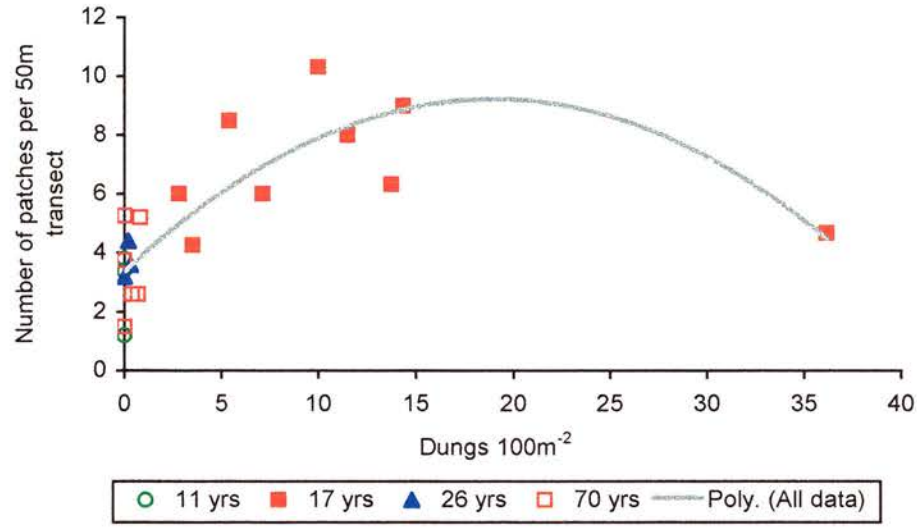


Figure 5.6 The relationship between grazing levels and patch number

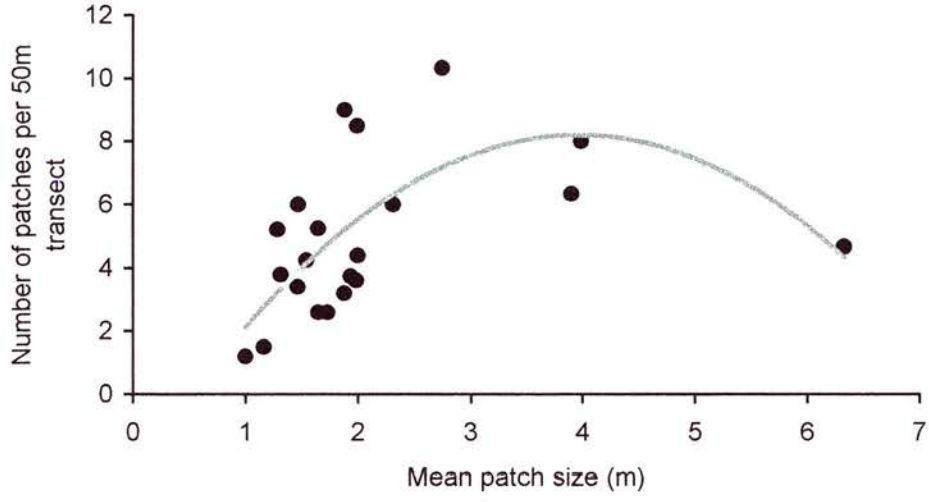


Figure 5.7 The relationship between patch size and patch number

Sequential Bonferroni Adjustments were made for this section, according to Table 5.2, and all values remained significant.

	Dung	Patch size
Patch area	<0.001	
Patch size	<0.001	
Patch nr	<0.001	0.006
Patch number r without Shed 2	0.04	
Vegetation height	<0.001	

Table 5-2 Summary of relationships in this section included in SBA. Figures given are P-values.

Thus it seems that grazing is important in determining the size, number and total area of patches less than 20cm high. Once again, all these effects were clearest at intermediate burn times. Although this is partly due to lower grazing levels in sites of other ages, it also seems likely that the intermediate aged sites are where grazing has the most impact on vegetation structure. In younger sites the vegetation is generally open anyway but grazing may slow down succession and prevent this developing into a continuous stand of shrubs. This is probably what has occurred at Haibar Nature Reserve (Figure 5.8), a site that was burnt in 1983 and completely protected from cattle and goats. It has very few open areas at all; the difference when compared to the Mitla sites, which were burnt just 6 years later but were grazed, is striking.

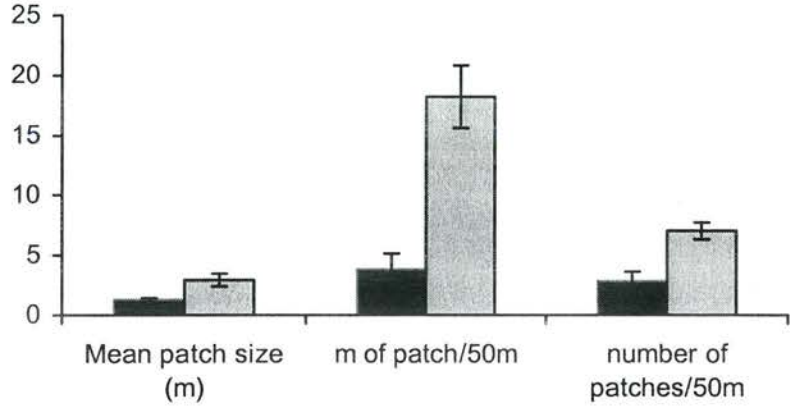


Figure 5.8 Patchiness at 11 and 17 year old sites, different burn times, showing the uniformity of vegetation height at Haibar (Black bars), relative to sites 6 years older (Mitla, MitShed and MitBot, grey bars).

Even if animals were introduced to a site after shrubs had grown, patches may gradually spread as animals browse from the edges of existing clearings. By the time the vegetation reaches maturity, grazing may have less impact on vegetation structure because the shrub layer becomes patchier anyway when trees take over as the dominant vegetation.

5.2.2 The effects of "patchiness" on flowers and bees.

The abundance and species richness of bees, herb flowers and total flowers were all increased by increasing patch size and the overall area of patch (although the relationship between bee abundance and patch size was not quite significant after SBA). All but flower abundance were increased by patch number (Table 5.3). The abundance and species richness of shrub flowers, on the other hand, were not at all affected by patchiness. (N.B. After SBA, the critical value of P is 0.0063).

	Flower species richness	**Flower abundance**	**Herb Species richness**	**Herb abundance**	**Shrub species richness**	**Shrub abundance**	**Bee species richness**	**Bee abundance**
Mean patch size	r_S=0.771 **P<0.000**	r_S=0.505 **P=0.004**	r_S=0.762 **P<0.000**	r_S=787 **P<0.000**	r_S=0.098 P=0.605	r_S=-0.337 P=0.068	r_S=0.738 **P<0.000**	r_S=0.482 P=0.007
Number of patches per 50m	r_S=0.747 P<0.000	r_S=0.384 P=0.036	r_S=0.702 **P<0.000**	r_S= 681 **P<0.000**	r_S=0.043 P=0.821	r_S=-0.239 P=0.202	r_S=0.522 **P=0.003**	r_S=604 **P<0.000**
Total m of patch per 50m	r_S=0.813 **P<0.000**	r_S= 0.497 **P=0.005**	r_S=0.768 **P<0.000**	r_S= 801 **P<0.000**	r_S=0.024 P=0.898	r_S=-0.337 P=0.069	r_S=656 **P<0.000**	r_S=0.513 **P=0.004**

Table 5-3. Spearman's Rank Order Correlations, relating "patchiness" to bees and flowers. All n=30. Those P values shown in bold were still significant after sequential Bonferroni adjustment, critical value, P= 0.0063.

Since patch size, patch number and the overall area of patch are all very closely related, it is hard to tell whether one has a stronger affect than others on flowers or bees. However, if patch number had a stronger effect than patch size, I would expect the relationship between bees or flowers and patch size to be unimodal, reflecting the relationship between patch size and patch number. This is in fact true when looking at total flower species richness, a polynomial curve (Figure 5.9a: PR: R^2=69.2%, n=21, P<0.001) fits better than a straight line (FTEST: F=19.38, DF=1,27, P=0.00015), an exponential curve (FTEST: F=27.02, DF=1,27, P<0.0001) or a one-

site binding hyperbola (FTEST: F=11.86, DF=1,27, P=0.0019). The same is true when herb flower species richness is plotted against dung levels. The data better fit a polynomial curve (Figure 5.9b: PR: R^2=69.3%, n=21, P<0.001) than a straight line (FTEST: F=18.94, DF=1,27, P=0.00017), an exponential curve (FTEST: F=27.81, DF=1,27, P<0.0001) or a one-site binding hyperbola (FTEST: F=13.92, DF=1,27, P<0.0001).

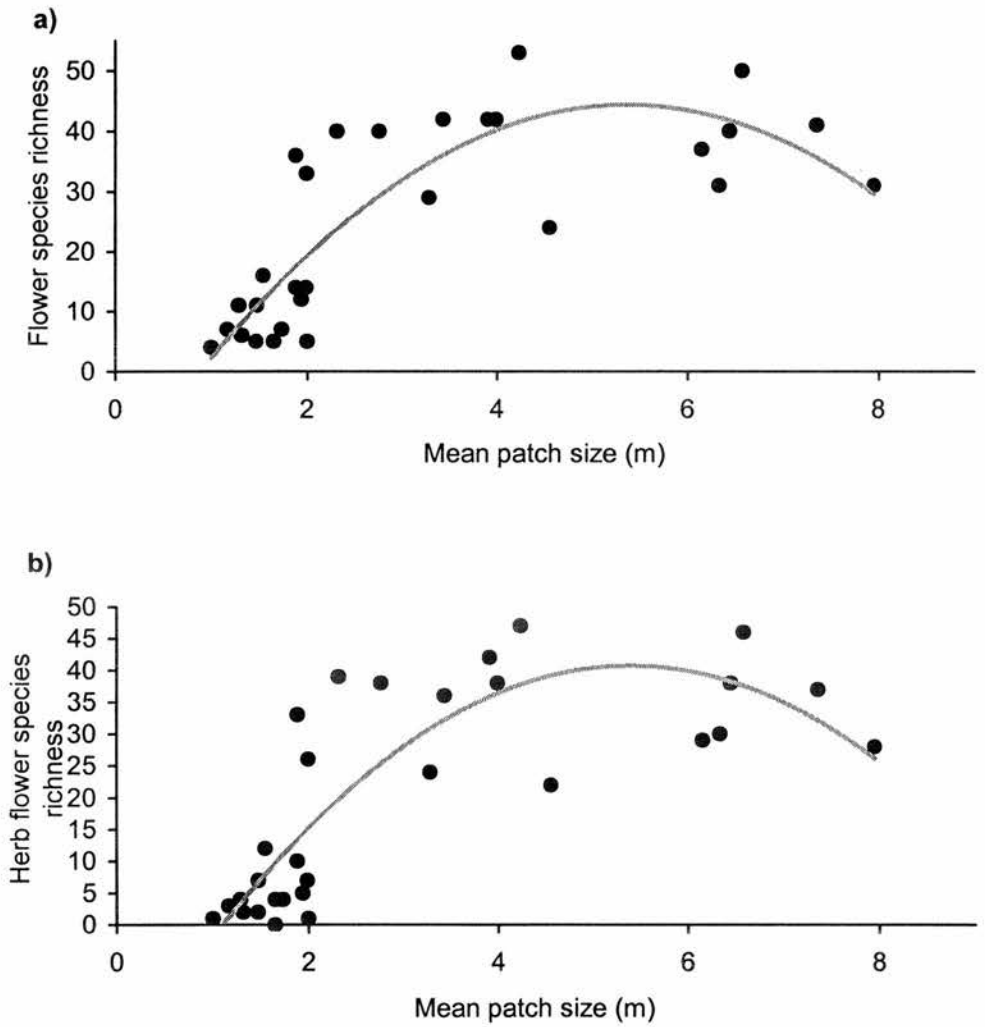


Figure 5.9. a) Total flower species richness and b) Herb flower species richness, plotted against patch size.

Hence, it seems that patch number is more important than patch size in determining species richness of total flowers and of herb flowers. This may be because it is not

only the open areas in the vegetation themselves which are important but also the number of edges, which may offer different niches. For overall flower species richness this is particularly important, because when patch number is highest, both shrub and herb species are still present. When patches get large enough to join together and patch number is reduced, some shrub species will have been lost so overall diversity will be reduced. For overall flower abundance, patch number was not important, which is presumably because the overall "open" area available to herbs, can support more flowers than if shrubs covered part of that area.

All three parameters are highly significant for bees and are probably functionally important in determining their abundance and species richness. The number of patches may be important to bees simply due to the increased abundance and diversity of herb flowers which can colonise open areas after removal of the dominant shrubs. However there may also be changes in the rewards provided by the shrubs at the edges of patches. The effects of "edginess" on rewards and pollinators were therefore investigated more specifically using *Lavandula stoechas* and *Cistus creticus* stands in Lesvos, Greece, in 2001. This is described in the next section.

5.2.3 Summary of Section 5.2

- Cattle grazing reduced vegetation height, but exerted its effect by opening up or keeping open patches within stands of shrubs, rather than decreasing the height of all vegetation.
- The size and overall area of patches under 20cm high increased with grazing levels. Patch number also increased but decreased again as patches got larger and joined together.

- All these effects were clearest in the intermediate aged phrygana.
- The species richness and abundance of herbs and bees were increased by the number, size and overall area of patches, whereas shrub flowers were not significantly affected.
- Flower species richness was affected more by patch number than by patch size, maybe due to the increased number of edges. For bees all measures of patchiness were important.

5.3 The effects of edginess on floral rewards and visitation.

5.3.1 *Lavandula stoechas.*

The size and distribution of *Lavandula stoechas* clumps were measured in a very "patchy" area of scrub and in one with very few open areas. The number of *L. stoechas* plants, flowers and flower spikes in each clump was recorded, as described in Chapter 2 (Section 2.2.3 c). Plants grew in very dense clumps and were hard to separate, so visitation to clumps was recorded rather than to plants, since this was also the unit most likely to be noticeable to a visitor. For visitation recordings, **edge** and **centre** clumps were paired. This was done by choosing two clumps with equal numbers of flower spikes, as individual flowers were too small to be counted without removing the spikes from the plant. Also, since all the flowers on a spike are extremely close together, the availability of rewards from each spike is probably more important to visitors than the availability from each flower. However, the flower spikes were picked following recordings on three of the observation days, so that a mean number of flowers per spike could be calculated for each watched plant.

5.3.1 a) Clump size, clump density, flower number and seed set

The distance between *L.stoechas* clumps was greater for edge clumps than for centre clumps (WSR: W=979.5, n=29,28, P=0.0276) and edge clumps were larger (WSR: W=992.0, n=29,28, P=0.0163) and tended to be made up of more individual plants, although this was not quite significant (WSR: W=1019, n=30,29, P=0.0547). Clumps at edges also had significantly more flowers per spike (WSR: W=1037, n=29, P=0.0049) and although the number of spikes per plant was not significantly different (WSR: W=9444.0, n=113,52, P=0.8210) there were more spikes per clump at edges (WSR: W=1120, n=30,29, P=0.0009). All these relationships are shown in Figure 5.10.

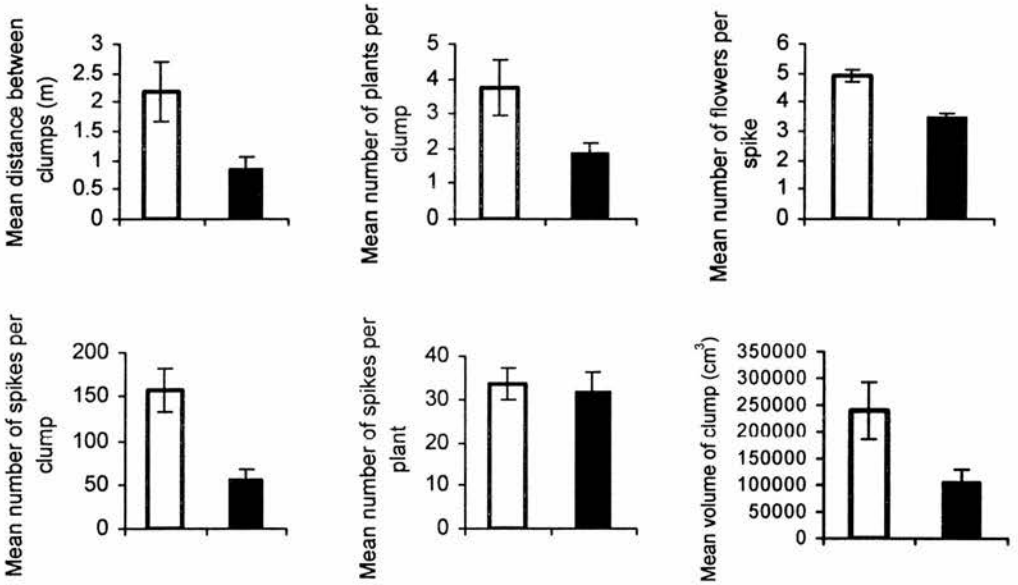


Figure 5.10 Differences between *Lavandula* plants in centre (black bars) and edge (white bars). N.B. all these variables except seed set were looked at in 30 edge clumps and 29 centre areas (see chapter 2). Number of flowers per spike were counted for up to 30 flower spikes from each plant.

5.3.1 b) Nectar

Nectar measurements were taken across four days using paired samples of 4 to 15 flower spikes from edge and centre areas at each sampling time (see methods, Section 2.2.3 a). Mean nectar volume per flower in *Lavandula stoechas* was highest at around

8a.m. and decreased quickly before 11 a.m. as shown in Figure 5.11 (SROC: r_S = -0.475, n=58, P<0.001). However the mean volume of nectar was significantly higher in flowers from the edges than in flowers from the central clumps at any one sample time (WSR: W=353, n=29, P=0.004).

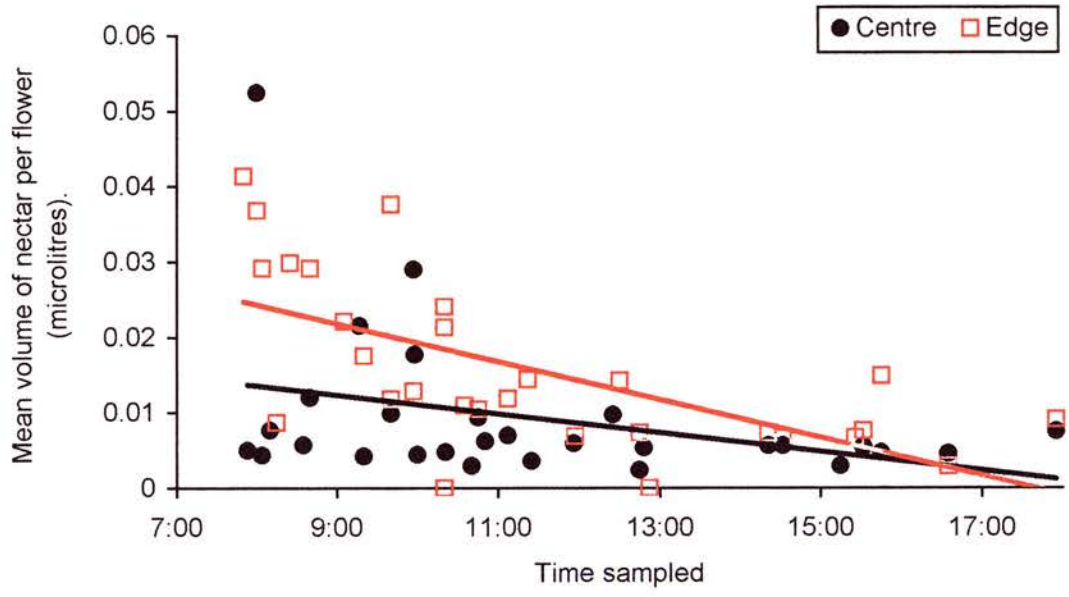


Figure 5.11 Mean volume of nectar per flower for each sampling time in centre and edge areas

Nectar concentration increased slightly throughout the day as shown in Figure 5.12, (LR: R^2=12.4%, n=56, P=0.008) but did not differ significantly between centre and edge clumps (Paired T: T=-0.84, n=28, P=0.406).

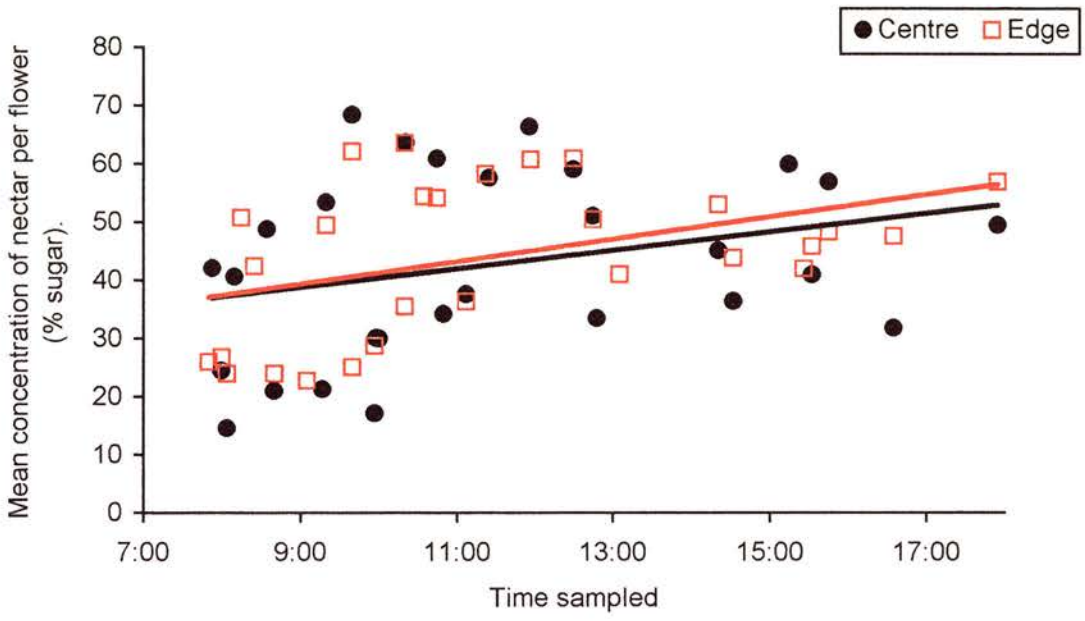


Figure 5.12 Mean nectar concentration per flower for each sampling time.

Since there was no difference in nectar concentration between the different areas, the difference in volume must reflect a higher rate of nectar secretion in edge flowers, rather than a difference in evaporation rates. The increase in nectar concentration during the day probably is due to evaporation, so that concentration is negatively related to volume. It appears that nectar concentration does increase slightly as volume decreases (Figure 5.12), although this is not significant (SROC: 0.206, n=56, P=0.127).

5.3.1 c) Visitation

Pairs of clumps with similar numbers of flower spikes were chosen for visitor observations. Since it was not possible to find clumps with exactly equal numbers of spikes, visitor numbers and visit lengths were divided by the number of spikes watched, to give a mean number per spike. All visitor numbers and visit lengths given are for a ten minute observation period.

A total of 545 visitors were observed, of which the majority (87%) were Apoidea, and the remainder were Diptera (11%), Lepidoptera (1%) and Coleoptera (1%). 39 % of all visitors were *Apis mellifera* and 25 % were *Anthophora spp.* A further 7% of visits were made by a species of bibionid fly; however these were excluded from the analysis since they always visited the "flag" on top of the flower spike (see figure 2.6), rather than the actual flowers, and therefore did not collect any rewards.

For all pairs of clumps observed over five days, there was no difference in number of visits per spike, between edge clumps and centre clumps (WSR: W=347.0, n=41, P=0.553). On three of the five days flower numbers were counted and there was no significant difference in the number of visits per flower (WSR: W=209.0, n=29, P=0.900). The mean duration of a visit to a clump was not significantly different between centre and edge patches (WSR: W=514.0, n=41, P=0.164) although there was a trend for visitors to remain longer at edge clumps as in Figure 5.13. Visit lengths per flower did not differ either (WSR: W=227.0, n=29, P=0.846).

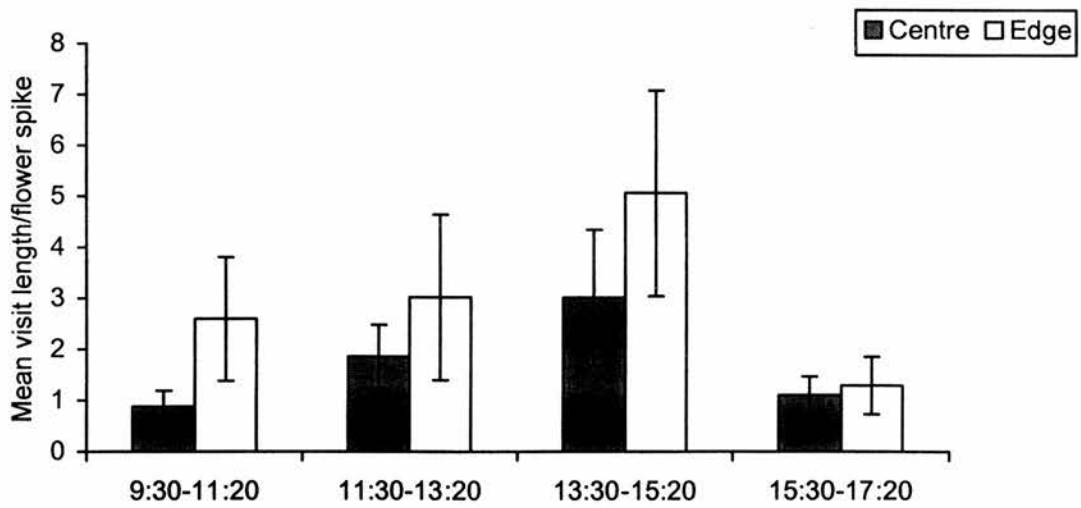


Figure 5.13 Difference in duration of visits/number of spikes in clump between centre and edge patches. Error bars show standard error across all clumps watched in one time period. These are relatively large due to variation between days.

5.3.1 d) Seed set

No significant difference was found for seed set between centre and edge clumps (Figure 5.14, T-test: T=0.17, n=50, P=0.86).

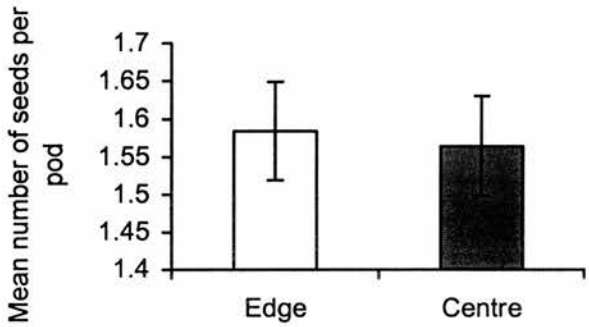


Figure 5.14 Seed set in centre (black bar) and edge areas (white bar). Seeds were counted in five pods on each of 50 randomly selected spikes

5.3.2 *Cistus creticus.*

This study took place in two different sites, as described in Chapter 2 (Section 2.2.4), and again compared rewards and visitation between *C. creticus* flowers in thick scrub and those on the edges of scrub patches.

5.3.2 a) Nectar

Only 15.25 % of the total 560 *C. creticus* flowers sampled contained measurable amounts of nectar. However at both study sites there was a higher percentage of flowers containing nectar in edge areas than in centre areas (N.B. Flower samples were paired with respect to day and sample time). At the Olive Grove site 18.8 ± 4.0 % of edge flowers and only 13.4 ± 3.7 % of centre flowers contained measurable amounts of nectar, although the difference was not significant (Paired T: T=1.65, n=16, P=0.059). At Vatera Hill 16.8 ± 2.8 % of edge flowers contained nectar, which was significantly higher than the 11.8 ± 2.7 % of centre flowers (Paired T: T=1.95,

n=14, P=0.037). On average then, nectar occurred in 17.8 ± 2.4% of edge flowers and 12.7 ± 2.3 % of centre flowers as in Figure 5.15, and again, the percentage of edge flowers containing nectar was significantly higher (Paired T: T=2.51, n=30, P=0.009).

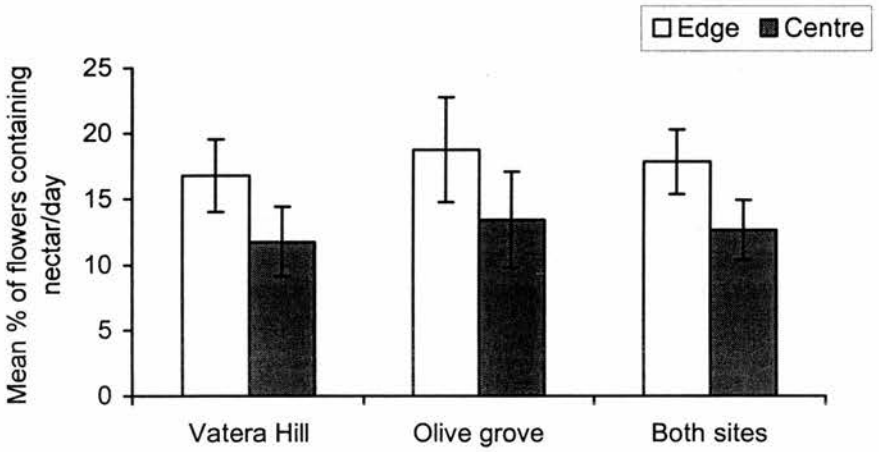


Figure 5.15 Percentage of flowers containing nectar. N.B. on each day samples of 20 flowers were taken 4 times a day so for analysis, samples were paired with respect to day and sample time. At Vatera Hill this was repeated on 3 days and at the Olive Grove it was repeated on 4 days. Standard Errors shown are across days sampled.

The mean volume of nectar per flower decreased slightly, but not significantly through the day (SROC: r_S=-0.152, n=30 P=0.189) as in Figure 5.16. However the large amount of variation between flowers means that more data would be needed to show any significant trend here. A pair-wise test (again flower samples were paired with respect to day and sample time), showed that at Vatera Hill the volume of nectar was generally greater in flowers from edges than in those from central areas (WSR: W=158.5, n=22, P=0.048), whereas at the Olive Grove site there was no significant difference between flowers from centre and edge areas (WSR: W=92.0,n=16, P=0.224). However when both sites were combined, volume was again significantly higher in edge flowers (Figure 5.16: WSR: W=524.5, n=38, P=0.003).

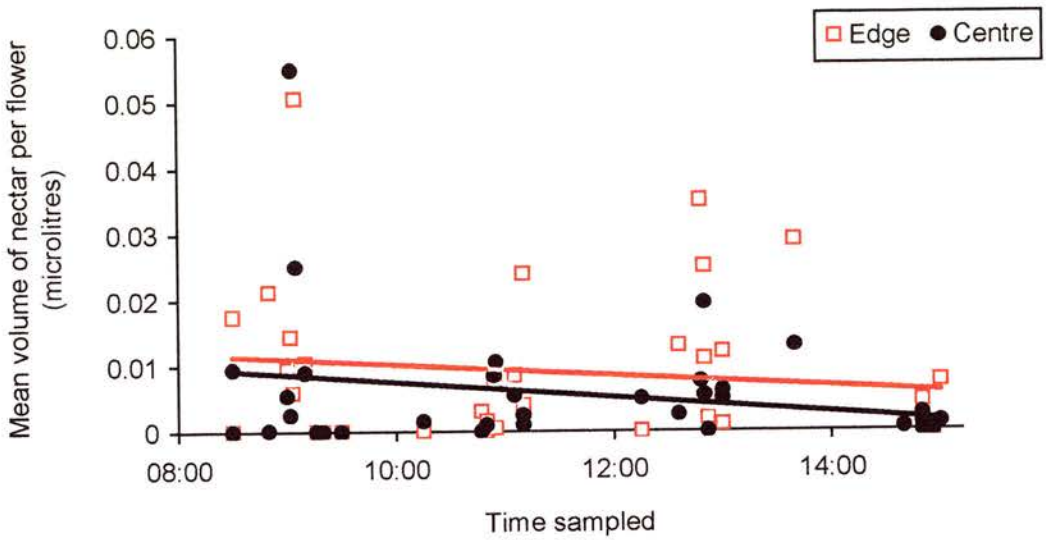


Figure 5.16 Nectar volume through time in centre and edge sites. N.B. Analysis was done using paired points for flowers sampled at the same time and on the same day.

Nectar concentration increased through the day (Figure 5.17, R^2=28.1%, n=45, P<0.001) but did not differ significantly between centre and edge patches at Vatera Hill (Paired T: T=0.31, n=12, P=0.765), at the Olive Grove (WSR: W=35.0, n=10, P=0.476), or with both combined (WSR: W=148.0, n=22, P=0.495).

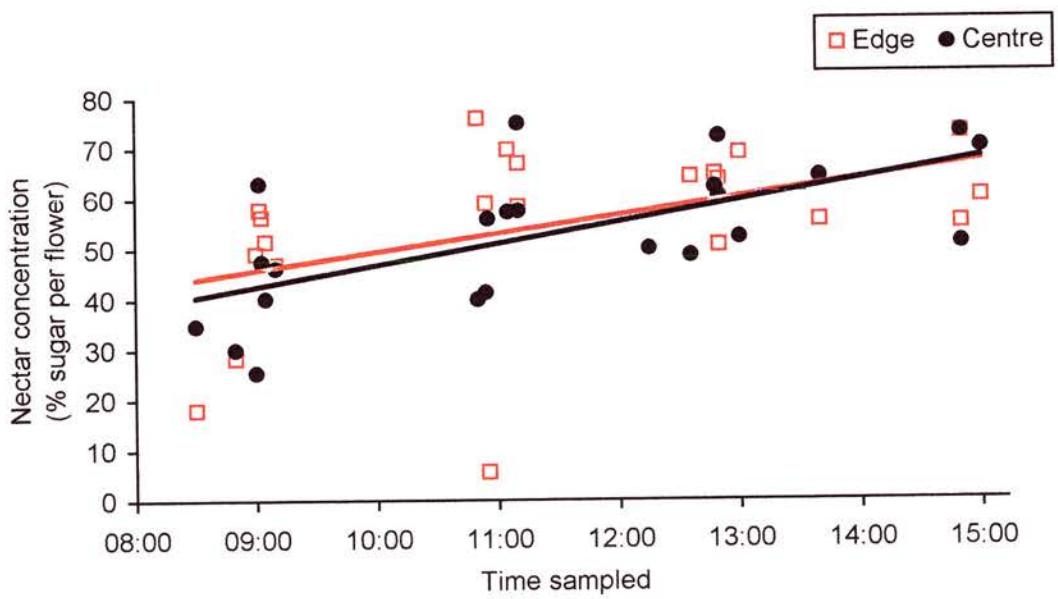


Figure 5.17 Nectar concentration through time in centre and edge sites. N.B analysis was done using paired points for flowers sampled at one time and on one day.

5.3.2 b) Visitors

A total of 568 visitors were observed. 37% of these were chafer and other pollen feeding beetles, and these were analysed separately. Of the remaining visitors, 79% were *Apis mellifera,* 12%, other bees, 4% Diptera, 2% Lepidoptera, 2% Coleoptera and 0.6% wasps.

Paired patches of flowers were watched, each with around 20 open flowers. However it was not possible to use exactly 20 flowers each time. To account for these differences the number of visitors to a patch was divided by the number of flowers, giving a mean number of visitors per flower. Visitor numbers are therefore given as number of visitors per flower, per 10-minute observation period. The total number of pollinator visitors per flower was almost significantly higher to edge flower at the Olive Grove site (WSR: W=376.0, n=37, P=0.09) but at Vatera Hill there was no significant difference (WSR: W=243.0, n=32, P=0.368). However when both sites were combined this gave a P value of 0.066 (WSR: W=1189.0, n=69), edge sites still having marginally higher visitor numbers as shown in Figure 5.18.

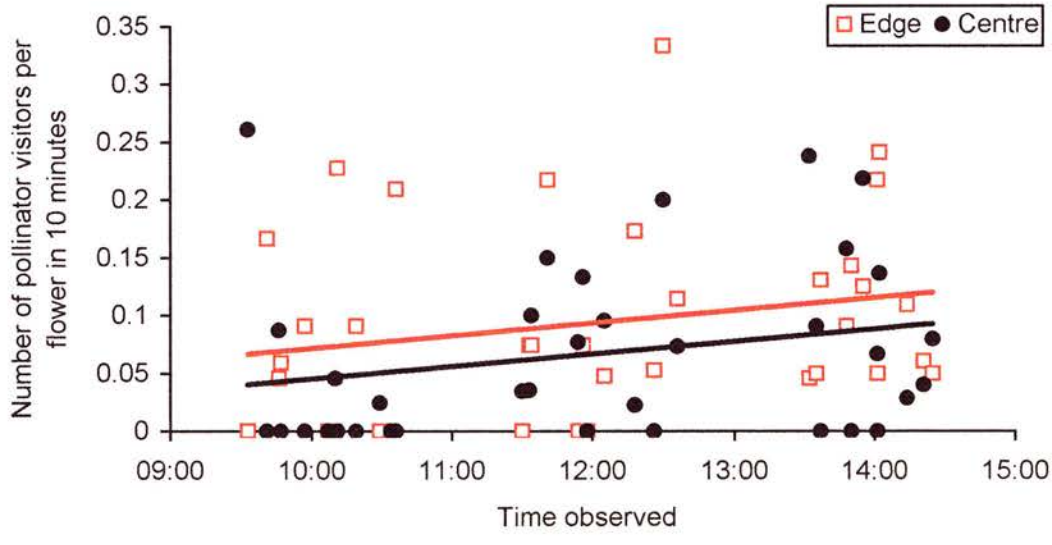


Figure 5.18 Number of pollinators per flower when both sites are combined (excluding pollen feeding beetles). N.B. For analysis, samples were paired with respect to time and day.

There was no significant difference in the number of pollen feeding beetles per flower between edge and centre flowers at either site (Both P>0.05). Visit length did not differ significantly in either site for pollinators or for pollen feeding beetles (all P>0.05); however the majority of pollen feeders stayed on a flower for the whole ten minute observation period so differences may not have been detectable.

5.3.2 c) Flower size and density

ANOVA (Figure 5.19, Table 5.4) showed that there were significantly more flowers per square metre at the edges of patches than in centre areas (P<0.001). Flower numbers were also higher at Vatera hill than at the Olive Grove site (P<0.001) and there was a significant interaction between site and area (P<0.001) showing that the difference between edge and centre areas was greater at Vatera hill.

Factor	DF	SS	Adj MS	F	P
Site	1	950.0	1150.8	18.18	**<0.001**
Area (Edge or centre)	1	13237.7	13293.3	209.98	**<0.001**
Interaction	1	1816.5	1816.5	28.69	**<0.001**
Error	748	47353.5	63.3		

Table 5-4 ANOVA for the effects of site and area on flower density in *Cistus creticus*.

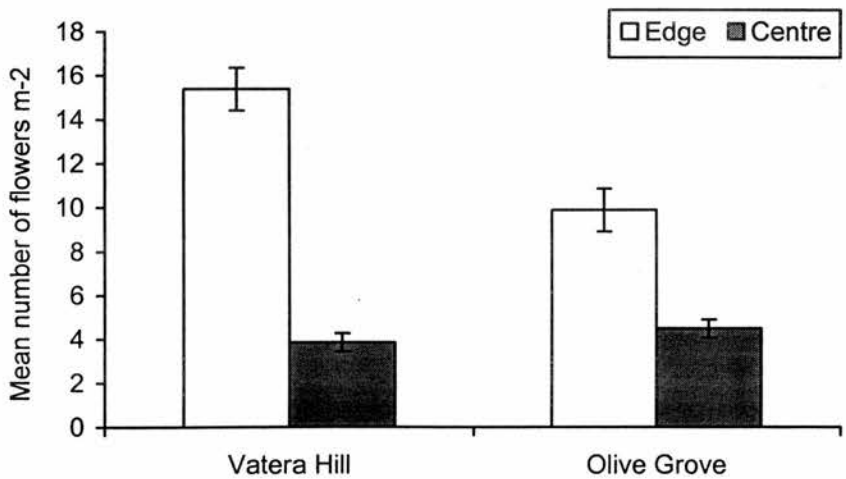


Figure 5.19 Flower density in centre and edge areas at both sites.

The sizes of *C. creticus* flowers were measured as described in Chapter 2 (Section 2.2.4 c). ANOVA (Table 5.5) showed that flower diameters were significantly greater on the edges than in the centre areas and that flowers were also larger at the Olive Grove than at Vatera hill (Figure 5.20, both P<0.001). There was no significant interaction between site and area (P=0.534) showing that the difference between edge and centre was similar in both sites.

Factor	DF	SS	Adj MS	F	P
Site	1	767.14	767.14	18.98	**<0.001**
Area (Edge or centre)	1	1374.30	1374.30	34.00	**<0.001**
Interaction	1	15.67	15.67	0.39	0.534
Error	374	15115.33	40.42		

Table 5-5 ANOVA for the effects of site and area on flower diameter.

The "flower centre" diameters (see Chapter 2, Figure 2.7) were also larger in edge areas (Table 5.6, P=0.009). Flower centre diameter was not significantly different between sites (P=0.873) and there was no interaction between the effects of site and area (P=0.927).

Factor	DF	SS	Adj MS	F	P
Site	1	0.114	0.114	0.03	0.873
Area (Edge or centre)	1	30.164	30.164	6.85	**0.009**
Interaction	1	0.037	0.037	0.01	0.927
Error	376	1656.869	4.407		

Table 5-6 ANOVA for the effects of site and area on centre diameters of *Cistus creticus* flowers

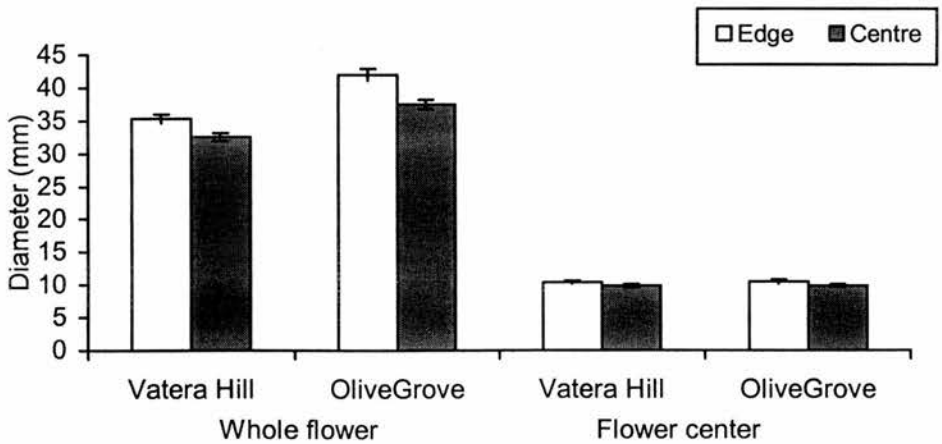


Figure 5.20 Flower diameter in centre and edge areas at both sites.

5.3.2 d) Pollen

ANOVA (Table 5.7) showed no difference in *C. creticus* pollen grain number between edge and centre areas (P=0.734). However Grain number was significantly higher at Vatera Hill than at the Olive Grove (P<0.001) and there was a significant interaction between the effects of site and area (P=0.023). See figure 5.21.

Factor	DF	SS	Adj MS	F	P
Site	1	$1.2076x10^{+10}$	$1.2076x10^{+10}$	13.51	**<0.001**
Area (Edge or centre)	1	103651370	103651370	0.12	0.734
Interaction	1	4791321007	4791321007	5.36	**0.023**
Error	106	$9.4769x10^{+10}$	894042477		

Table 5-7 ANOVA for the effects of site and area on pollen grain number.

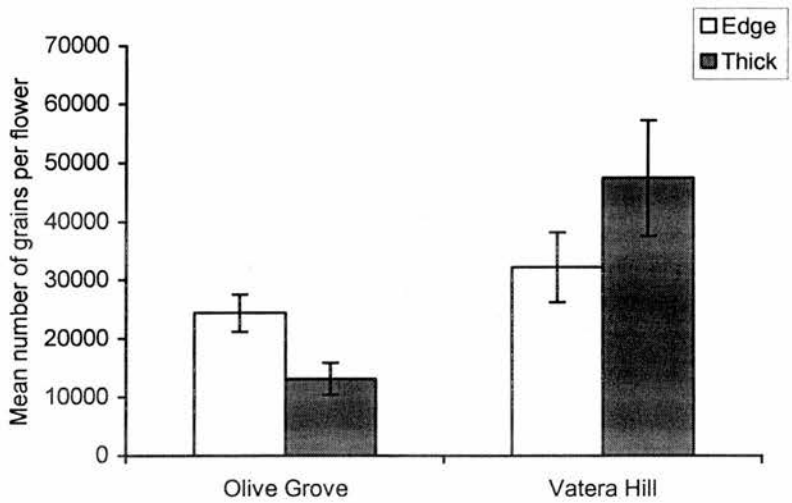


Figure 5.21 Number of pollen grains per flower in centre and edge areas.

ANOVA (Table 5.8) showed that there was no difference in *C. creticus* pollen grain diameter, between edge and centre areas (P=0.352) but that grains were slightly larger at the Olive Grove than at Vatera hill (P=0.041) and there was a significant interaction between the effects of site and area (P=0.039). See Figure 5.22.

Factor	DF	SS	Adj MS	F	P
Site	1	13.149	13.149	4.30	**0.041**
Area (Edge or centre)	1	2.667	2.677	0.88	0.352
Interaction	1	13.423	13.423	4.39	**0.039**
Error	99	302.783	3.058		

Table 5-8 ANOVA for the effects of site and area on pollen grain diameter.

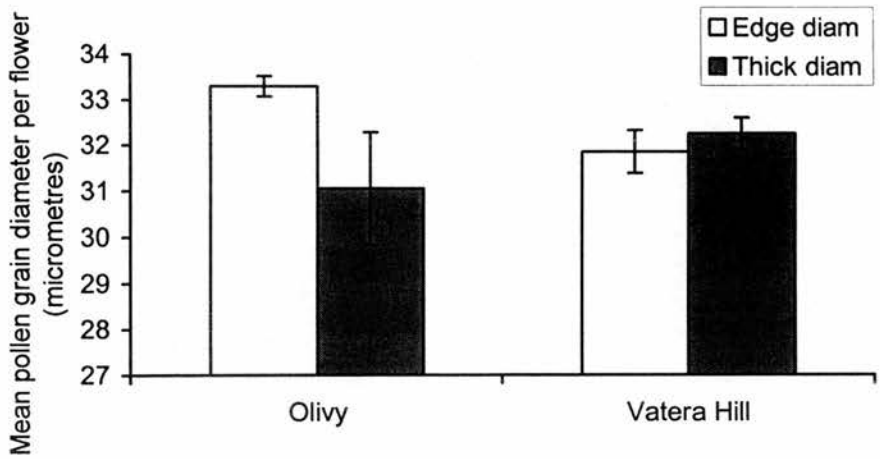


Figure 5.22 Mean pollen grain diameter in centre and edge areas.

The results for the numbers (Figure 2.21) and diameters (Figure 2.22) of pollen grains at Vatera Hill seem to go against the general trends found so far in this section. Pollen at Vatera Hill was collected on two days, the first of which was very windy. It may be that on this day less pollen was removed, since the pollinators were unable to fly. When grain numbers on the two days were compared (Figure 5.23, Table 5.9) there was still no difference between edge and centre areas (P=0.207) but there **were** significantly higher pollen grain numbers on day one (the windy day) than on day 2 (P=0.001).

Factor	DF	SS	Adj MS	F	P
Site	1	2154564105	2154564105	1.64	0.207
Area (Edge or centre)	1	$1.5512x10^{+10}$	$1.5512x10^{+10}$	11.82	**0.001**
Interaction	1	3352932105	3352932105	2.55	0.117
Error	46	$6.0375x10^{+10}$	1312491401		

Table 5.9 ANOVA for the effects of day and area on pollen grain number at Vatera Hill.

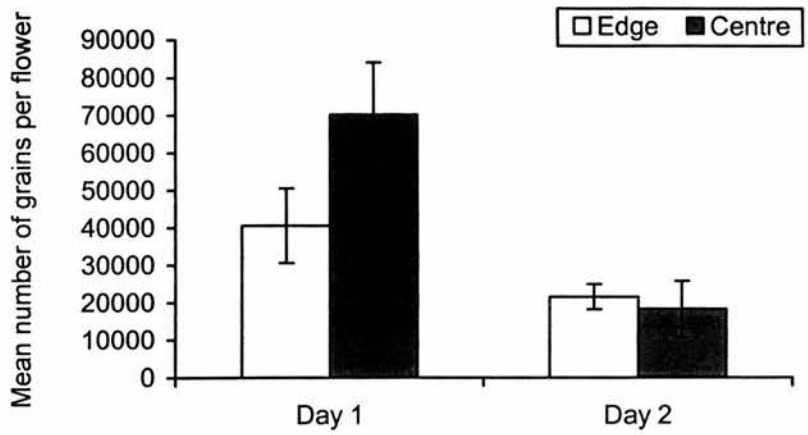


Figure 5.23 Number of pollen grains per flower in centre and edge areas, on two separate days at Vatera Hill.

Unfortunately, another possibility is that the samples from day 1 on Vatera hill were incorrectly labelled and that the trend should be in the opposite direction, therefore this study needs to be repeated to obtain a conclusive result.

5.3.2 e) Soil

As shown in Table 5.10, soil properties in different areas were relatively similar. The only clear difference was that the edge areas in the Olive Grove were relatively high in potassium, whereas the centre areas here, and both areas at Vatera Hill were low in potassium.

Site	Area	Nitrogen	pH	Phosphorous	Potassium
Olive Grove	**Edge**	Medium/Low	>7.5	Medium	High/Medium
	Centre	Low	>7.5	High/Medium	Very Low
Vatera Hill	**Edge**	Medium/Low	>7.5	High/Medium	Low
	Centre	Medium/Low	7	Medium/Low	Low

Table 5.10 Soil constituents at edge and centre areas of Vatera Hill and Olive Grove sites.

5.3.3 Summary of Section 5.3

- Overall there were clear differences in floral rewards and visitation between edge and centre areas for both *Lavandula stoechas* and *Cistus creticus*.

- *Lavandula stoechas* clumps contained more flowers overall at edges, although these clumps were further apart than centre clumps were. The density of *Cistus creticus* flowers was also greater at edges of patches, and the flowers were larger.
- Both species had greater nectar rewards at edges. *Cistus creticus* also appeared to have differences in pollen grain number and size between edge and centre areas but the trends were opposite in different sites and there were also differences between sample days so this result was inconclusive.
- The number of visitors to edge spikes tended to be higher than to centre spikes in *Lavandula stoechas*. In *Cistus creticus*, visitor numbers also tended to be higher to edge flowers, although neither of these results were significant.
- On the whole, an increase in the number of edges in phrygana is probably an advantage to visitors of shrubs, since the high density of flowers at edges, together with the increased rewards per flower, mean that more energy can be obtained with less travelling time.
- This means that patchiness may benefit those bees which visit shrubs as well as those which benefit from the increase in herb flowers within the open patches.

5.4 Discussion

5.4.1 The effects of grazing on vegetation structure in Israel

Grazing was found to decrease the mean height of vegetation, particularly in the intermediate aged sites. When looked at in more detail, it seemed that the effect of grazers was to inhibit the growth of shrubs in various patches, rather than decreasing

the height of all the vegetation. This probably took place by repeated grazing and trampling of the same patches, beginning before the shrubs became full sized and therefore inhibiting their growth in some areas. Since cattle prefer to feed on graminoids than on shrubs (Damahoureyeh & Hartnett 1997), they would have repeatedly returned to previously grazed patches therefore keeping them open even when the neighbouring shrubs were mature.

Although cattle are known to avoid feeding on woody plant types, they may do so when there is no alternative food plant (Harrington, 1982; Augustine *et al.* 1998) or when they are unable to move elsewhere. This was also noted by Eli Sandovski (a cattle farmer on Mount Carmel, Israel). He had observed that although his cattle would not normally feed on *Cistus* bushes, they did so in the middle of summer when all other vegetation had dried up, at which point the stocking density was very high, relative to the amount of herbaceous vegetation available. This means that those shrubs which were not prevented from growing in the first place may still have been reduced by defoliation in mid-summer and mid-winter. Cattle in Israel were also observed pushing their way through thick vegetation, breaking bushes in the process, so this was yet another way in which open patches could have been created.

Overall, the total area of vegetation under 20cm high and the total size of open patches were increased by grazing. However patch number was highest at intermediate grazing levels, then decreased again as patch size increased and patches began to merge together. This means that the total amount of vegetation less than 20 cm high was greatest at the highest grazing levels, but that the most variation in vegetation height and the most edges occurred at moderate grazing levels.

All these effects were clearest in the intermediate aged sites, which was due partly to the fact that these sites were more heavily grazed than the rest, and partly to the fact that rather than an overall reduction in height of all vegetation, the decrease in height was caused mainly by the removal of shrubs. In the most recently burnt sites, intense fires had already removed the dominant shrubs (as discussed in the previous chapter). Cattle could therefore change the species composition by preferentially selecting certain plant species, but could make little difference to the overall species richness or structure of the vegetation. In the mature sites, the understorey vegetation has open patches anyway due to shading by trees. Cattle grazing may further increase this "patchiness", but as the mature sites in this study were almost completely ungrazed, I have no data to support this.

5.4.2 The relationships between vegetation "patchiness" and the diversity and abundance of bees and flowers

The abundance and species richness of bees, herb flowers and total flowers all increased with the total area of vegetation under 20cm high, yet the abundance of shrub flowers was not affected by any measure of "patchiness". This seems surprising at first since the increasing area of short vegetation with higher grazing levels would suggest that the overall cover of shrubs must have been decreased. However if the density of flowers was increased at the edges of shrub patches as was found for *Cistus creticus* (Section 5.3.2), then this would make up for the overall reduction in the cover of shrub plants. This must explain why the abundance of shrub flowers did not decrease when the area of short vegetation increased. However it seems that the additional numbers of flowers at the edges of patches are not as high as

the numbers of herb flowers would be if all the shrubs were removed, since overall flower abundance is explained by patch size and patch area, but not by patch number.

Since the relationships between flower species richness and patch size are unimodal, as is the relationship between patch number and patch size, patch number must be the best predictor of flower species richness. This makes sense for overall flower species richness, because if the patches increased in size until they began to join together and patch number was reduced, then shrubs species would be lost and therefore overall floral diversity would be reduced. Herb flower species richness was also better explained by patch number than by the total area of patch, which is probably due to the increased number of edges between open areas and scrub areas. This fits with previous work showing that diversity is often highest at "edges" (e.g. Leopold 1933; Harris 1989).

For the diversity and abundance of bees, the number, size and total area of patch all seem to be equally important. Since the number of patches appears to be no more important than the total area of patch, this suggests that the edginess of the habitat is not important to bee communities. The limiting factor must therefore be the total availability of flowers, rather than the shelter or nesting sites provided by the shrubs. However the most heavily grazed areas still had at least 40% shrub cover and even the freshly burnt areas had over 20%, so these probably provided all the necessary shelter.

It seems then that the levels of disturbance in the sites included in this study do not limit bee communities by removing shrub cover. However, if both fire and grazing become more intensive, or more frequent, this may result in areas where shrubs have

been completely removed and where bee diversity **is** limited by the availability of nesting sites and shelter provided by shrubs. It seems likely therefore, that bees benefit from the increased area of short vegetation, mainly due to the increasing abundance of herb flowers, as was shown in Chapter 3. Nevertheless, those shrubs which are left on the edges of open patches may still be important, as was shown by the studies of *Lavandula stoechas* and *Cistus creticus* discussed in the next section.

5.4.3 The effects of edginess on floral rewards and visitation

5.4.3 a) *Lavandula stoechas*

Although the clumps of *L. stoechas* were more spread out in the patchy area than in the denser scrub, there were more plants and more flower spikes in each clump and therefore a higher number of flowers concentrated in one place. This means that although edge clumps were further apart, a visitor to an edge clump would find more flowers in a small area than a visitor to a centre clump would.

Nectar availability was difficult to measure in *L. stoechas*, since volumes were small and many flowers contained no nectar at all. The volume of nectar also decreased quickly before 11 am, mainly due to evaporation. However at any one sample time, flowers from edges of patches did contain more nectar than those in thick scrub, and since concentration did not vary between the two areas, this must have been due to increased sugar production by edge flowers, rather than to differences in evaporation rates.

In spite of the greater nectar rewards at the edges of patches, the frequency and duration of insect visits per flower was not increased and neither was the frequency of

visits to any one clump (matched for number of flower spikes). There **was** a tendency for visitors to remain longer at edge clumps, although this was not significant. It is likely that visitors spent more time at edge clumps, because of the higher flower numbers. Given that the duration of visits to each flower was no higher at edges, it seems that the increased availability of nectar in each flower made no difference. This may be because a flower took a given length of time to visit, regardless of whether or not a reward was obtained.

Since the number of visitors to any one clump was no greater in edge areas, it seems that edge clumps were no more visible than centre clumps; so although there were more rewards available from edge clumps, visitors could not tell this at a distance. This also suggests that there may have been no benefit to the plant from being at the edge of a patch and from producing higher nectar rewards. However, the number of seeds per pod was equal in both areas, and since edge plants had more flowers on each spike it is likely that edge plants produced more seeds overall.

5.4.3 b) *Cistus creticus*

In *Cistus creticus,* more flowers contained measurable amounts of nectar in edge areas and the average nectar volume per flower was greater. Nectar concentration did not differ between the two areas, showing that the higher volumes from edge flowers resulted from increased nectar production. There were also more flowers per square metre on the edges of open patches and these flowers had greater diameters and tended to also have larger centres. All of these factors suggest that the plants were investing more energy in flowers at patch edges. The greater size and numbers of flowers would provide a better "flag" to visitors at the edges of patches making them

more visible from a distance.

For pollen production, however, the results were less clear. At the Olive Grove, edge flowers tended to have more pollen grains and these were larger whereas at Vatera Hill the trends were in the opposite direction so that overall there were no significant differences between pollen rewards from centre and edge flowers. Pollen grains from edge flowers at the Olive Grove were also larger than in either area at Vatera Hill, which could have been due to differences in soil nutrients (i.e. high potassium) at edges in the Olive Grove. This could also explain the fact that flowers were larger in edge areas at the Olive Grove than either in centre areas or at Vatera Hill. However this idea is contradicted by the fact that both pollen grains and flowers were more abundant at Vatera Hill than at the Olive Grove. It therefore seems likely that the inconsistency in these results between sites is the result of random variation, and too small a sample size for pollen rewards.

Overall, edge plants produced more flowers in a smaller area, they were larger and more visible and they provided greater nectar rewards and possibly greater pollen rewards as well. In spite of this, the number of pollinator visits per flower was only marginally higher at edges and the difference was not significant. The duration of visits did not differ at all, but this may have been because where rewards were small, visitors spent more time searching for them and where they were large, time was spent collecting them.

Since this data was collected, there has been further work done on nectar production in *Cistus creticus*. Manetas & Petropoulou (2000) found that *C. creticus* flowers

produced significant amounts of sugar which were not measurable using micro-capillaries (the method used in this study). They also found that increasing nectar yield artificially did increase the duration of bee visits. In the present study it may be that the samples obtained were only from those flowers containing unusually dilute nectar which was easier to sample. Nonetheless, there **was** a difference in the amount of measurable nectar between centre and edge areas, which could be because more water was available to edge plants.

Even if the measurements of nectar and pollen were not accurate enough to be conclusive, it is surprising that the increases in flower size and density at patch edges made no difference to visit frequency or duration. However this is probably due to the way the data were collected. Visitation was recorded per flower, rather than per unit area or per plant. This means that at the edges of patches, where flowers were denser, there were in fact more visitors per unit area, and probably per plant as well.

Typically, the density of flowers per square metre was much higher at edges than in centre patches. However in order to observe visitors, paired groups of flowers were selected, with similar flower numbers, and where around 20 flowers could be watched at one time. This meant that although flowers in the centre areas were more spread out, those clumps selected for observation tended to be where the flowers were denser than average. The results were therefore biased, since these plants may have been particularly healthy or unusual in some way and may have had larger flowers and offered higher rewards than those observed in the general "centre" population, so they could therefore attract more visitors. More visitors may have also been attracted simply because there was a large group of flowers close together. Single flowers,

more typical of the centre areas would probably have brought in fewer pollinators since they were less obvious and since visitors would have to travel further between flowers. However observing these would have been impractical in this study, due to the hours of watching necessary to record a significant number of visits to a single flower.

5.4.4 a) Grazing, vegetation structure and pollinators

Overall then, the effect of grazing was to inhibit the growth of some of the shrub species in intermediate aged sites, thereby creating open patches within the taller scrub. The removal of the dominant shrubs in these areas and the increase in the number of edges allowed an increase in the diversity and abundance of herb flowers as well as increased production of rewards by shrubs at the edges of patches. Altogether the increased vegetation heterogeneity caused by grazing animals, led to an increase in the diversity and abundance of rewards and therefore an increase in the diversity and abundance of bees.

6 Goat grazing on Lesvos

6.1 Introduction

Since studies in Israel included only one very highly grazed site and did not cover the full range of grazing levels in between, I had aimed to return to Israel in 2001and to carry out a more thorough survey of grazing and survey of flowers. This would have concentrated solely on the 17 year old sites and covered as great a range of grazing levels as possible. This way I hoped to show more clearly the unimodal relationship between flower species richness and grazing, and if possible, to find out at what level grazing had a negative effect on floral abundance. However I was unable to return to Israel so I carried out a similar survey on Lesvos, where the main grazers were goats rather than cattle.

Domestic goats have gained a bad name for contributing to habitat degradation and erosion in Mediterranean habitats (Walter 1968; Giorgia *et al.* 1998; Hill *et al.* 1998; Perevolotsky *et al.* 1998) but this is probably due to the fact that grazing and browzing have often been very intensive. It is likely that at lower levels of grazing, goats would increase floral diversity as cattle did in Israel. However goats feed preferentially on woody species (Perevolotsky *et al.* 1998) and can bite closer to the ground than cows (Harrington *et al.*, 1982) so it is possible that goats have more destructive effects on vegetation than do cattle. In this study I aimed to find out whether floral diversity in phrygana was highest at intermediate levels of goat grazing, as it was for cattle, or whether even at low levels grazing had a detrimental effect.

Nine sites were surveyed on three days each (between the 6th of April and the 13th of May), all in one area burnt in 1977 (24 years previously). At each site a 60m transect was set up and split into three 20m sections. Grazing levels, vegetation structure and flower diversity and abundance were measured along these, as described in Chapter 2 (Section 2.3). The three 20 m transects in each site are given as separate points in this analysis since grazing levels were quite variable between the different sections. All the transects were perpendicular to the road, and many seemed to be more heavily grazed in the section closest to the road. Note that because goat dung pellets are very small and were very abundant they could not be counted accurately, therefore, grazing levels in this chapter were measured as the percentage of quadrats containing dung, rather than the total number of dung samples as in previous chapters.

6.2 Goat grazing and flora

Figure 6.1 shows that the number of flower species increased with grazing (LR: R^2=21.7%, n=27, P=0.015). However total flower cover (cm^2, see Section 2.3) was not significantly related to grazing intensity (SROC: r_S=0.004, n=27, P=0.984).

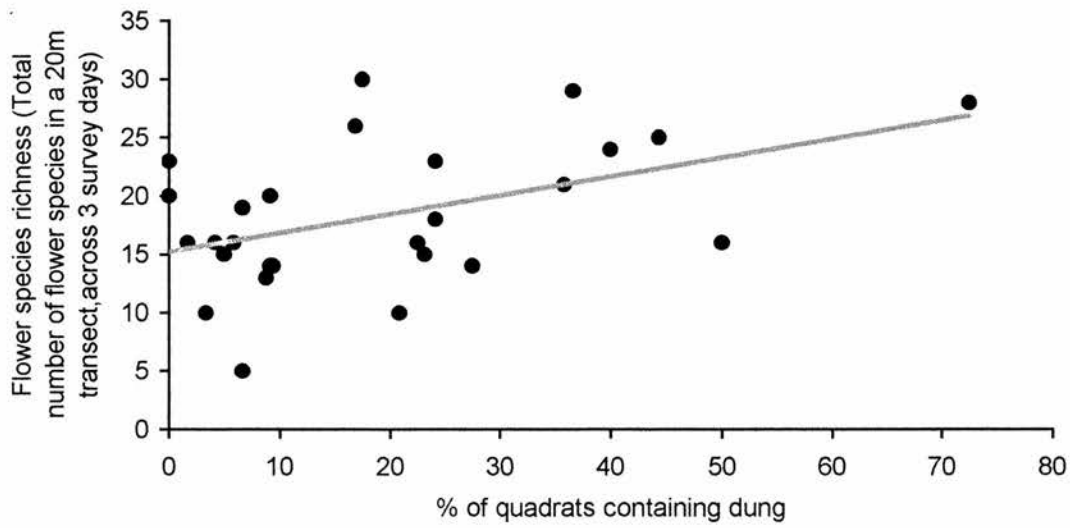


Figure 6.1 The relationship between flower species richness and goat grazing levels. Three separate points are given for the three 20m transects in each site.

6.3 Goat grazing and vegetation structure

Vegetation height was measured at points every 0.5 m along the transect. Mean vegetation height was found to decrease with grazing intensity as in Figure 6.2 (LR: R^2=18.6%, n=27, P=0.026).

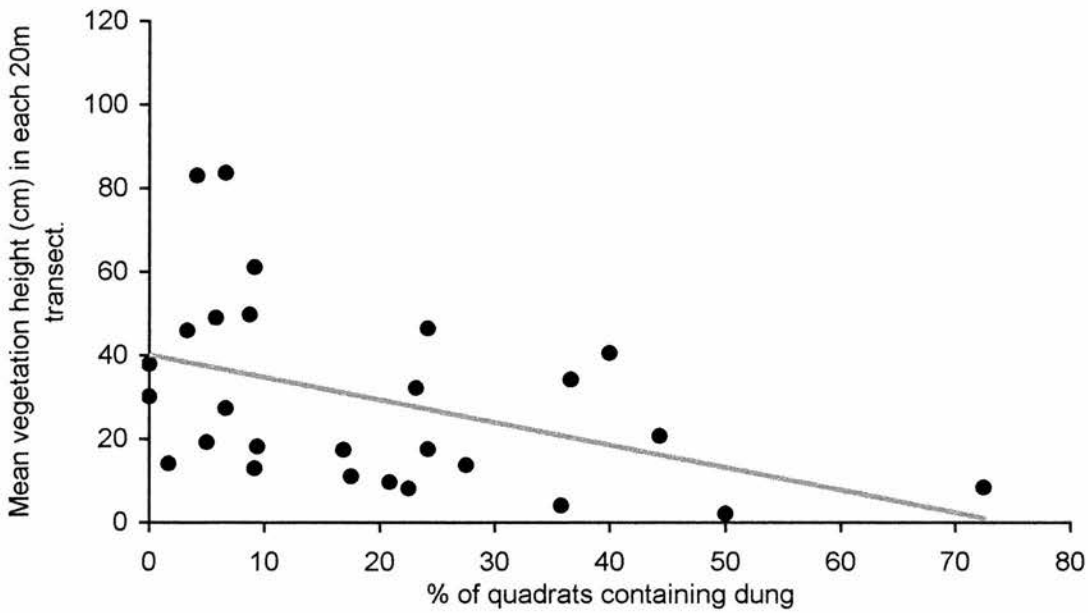


Figure 6.2 The relationship between goat grazing intensity and vegetation height.

As in Israel (Chapter 5), there was considerable variation in "patchiness" across sites, and two examples are shown in Figure 6.3.

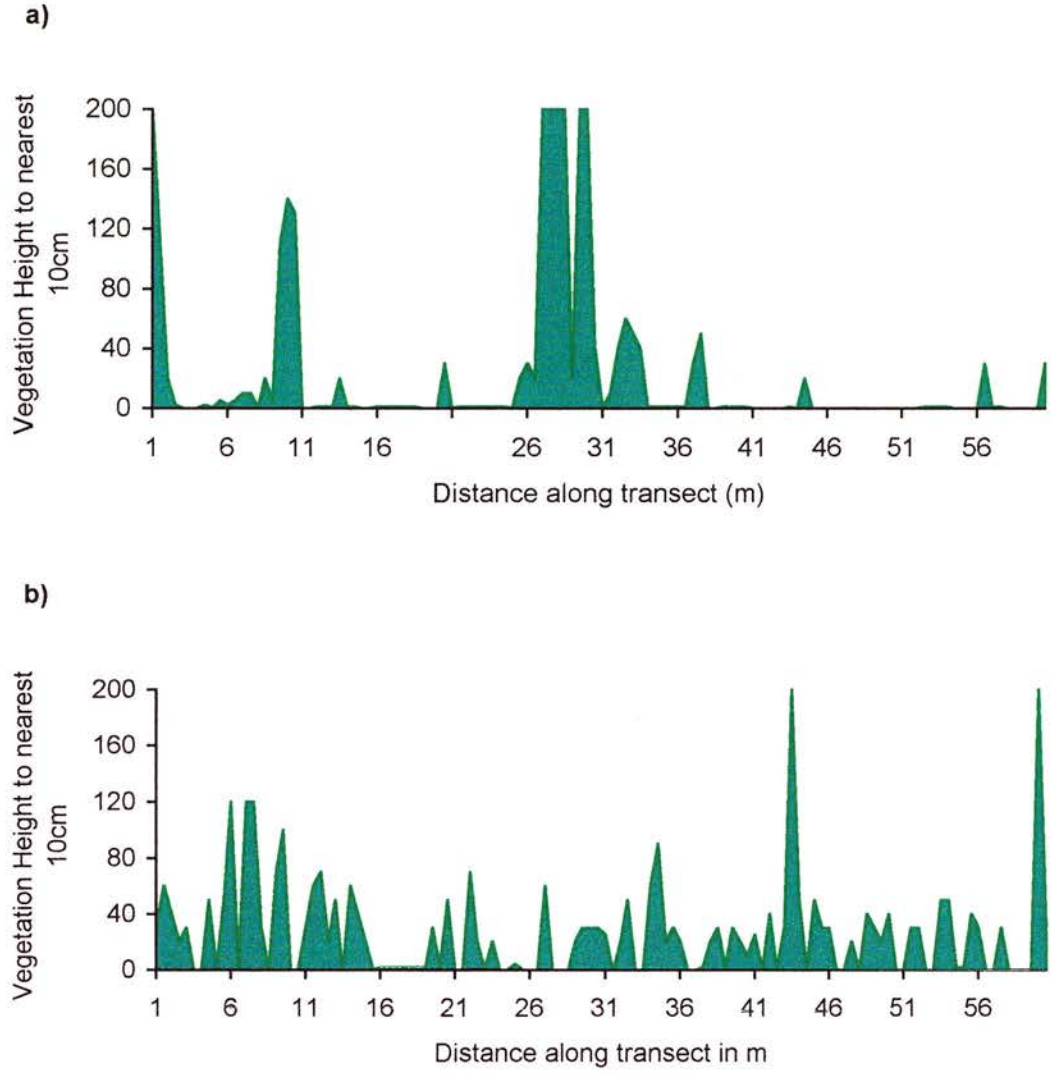


Figure 6. 3 Cross section of vegetation at (a) Site 8, with patches of bare ground and 44.97 ± 2.89 % dung and (b) Site 5, with fewer bare patches and 17.98 ± 5.66 % dung. N.B. Points show on graph as 200 cm high are 200cm or taller.

For the vegetation height surveys in Israel, no data were collected on plant type at each point. On Lesvos, however, each time the height of a plant was measured, it was recorded as either herb or shrub (or bare ground or rock). Since in Israel cattle were found to open up patches within stands of dominant shrubs, allowing more herbs to establish, it was important for comparison with cattle grazing effects, to look at the

patches of herbs and bare ground at each site. 95% of herbs were found to be under 10cm high so this was the height used to differentiate between "patch" (open areas) and "non-patch" (areas with thick scrub cover) in this study.

The proportion of patch <10cm high was found to increase significantly with grazing level (Figure 6.4 **a**, LR: R^2=20.1%, n=27, P=0.019), although this relationship was very much less clear than in Israel, where cattle grazing explained 49 to 78% of the variation in proportion of patch. Patch number was not affected by grazing (Figure 6.4 **b**, LR: R^2=3.3%, n=27, P=0.361) and neither was patch size (Figure 6.4 **c**, SROC: r_S=0.326, n=27, P=0.097), although patch size did show a tendency to increase with increasing grazing levels.

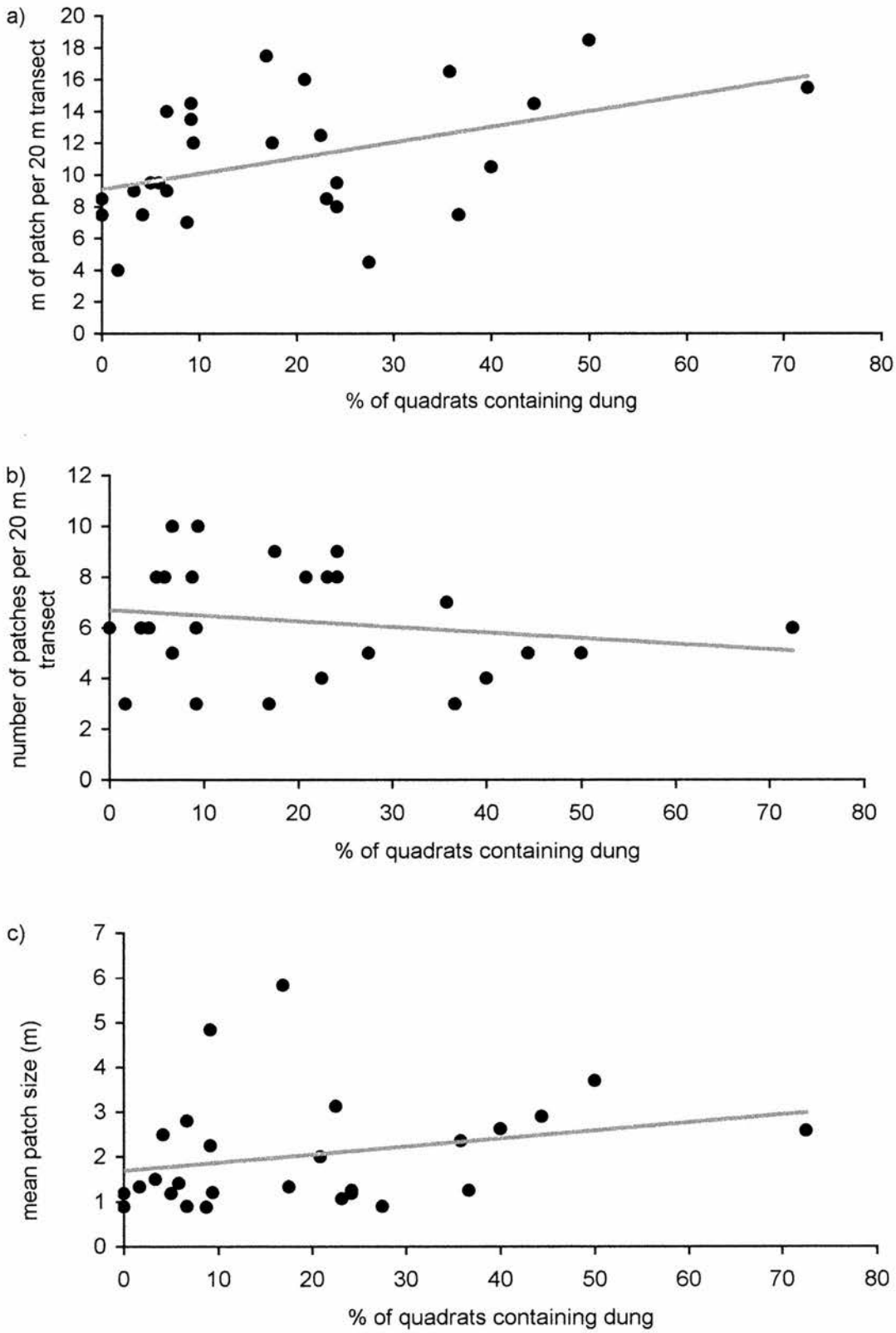


Figure 6.4 a) proportion of patch, b) number of patches and c) mean patch size, plotted against grazing intensity.

However, neither the number of flower species nor total flower cover were significantly related to patch area or patch size (SROC: all P >0.05), though flower species richness did show a positive trend with patch size, but the correlation was not significant (Figure 6.5, SROC: r_S=0.370, n=27, P=0.057). Flower cover actually decreased significantly with the number of patches (Figure 6.6, SROC: r_S=-0.417, n=27, P=0.030) and flower species richness decreased almost significantly with the number of patches (LR: R^2=13.2%, n=27, P=0.063).

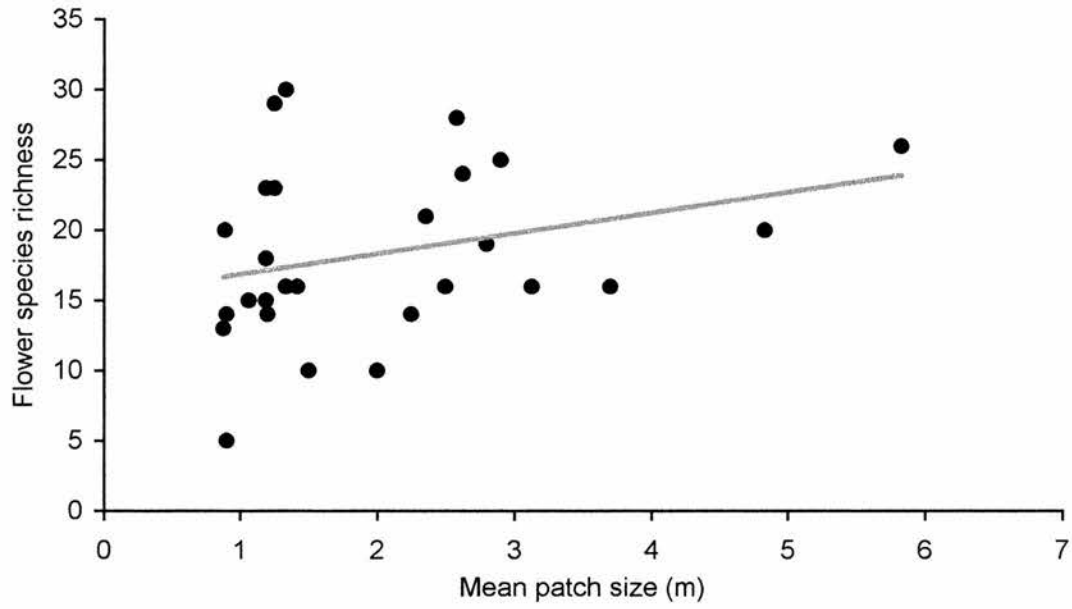


Figure 6.5 The relationship between mean patch size and flower species richness

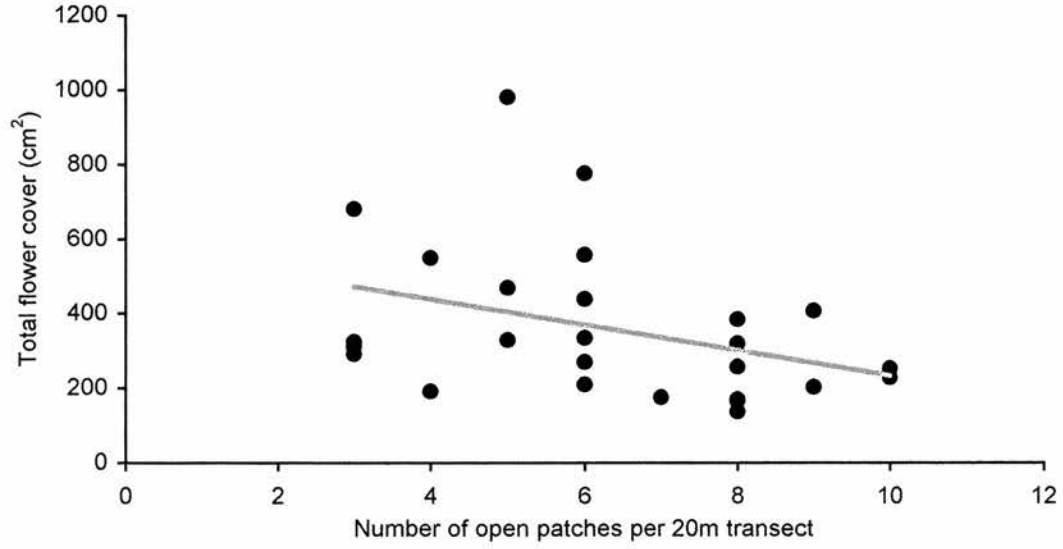


Figure 6. 6 The relationship between flower cover and patch number

Bare rock made up 19.7 (± 4.05) % of the open areas in all these sites combined and bare soil made up 18.2 (± 4.3) %, the remaining 60% being low vegetation. It is possible that grazers actually increase the amount of bare rock or shallow soil, since trampling and removal of vegetation may allow the topsoil to be eroded away. The area of bare rock did increase significantly with grazing intensity (Figure 6.7 SROC: r_S=0.573, n=27, P=0.002).

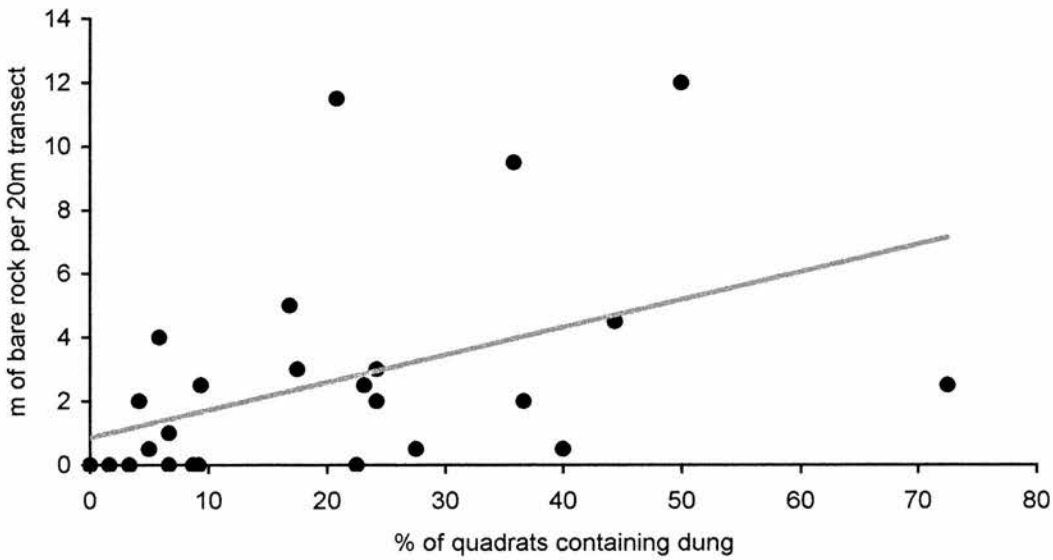


Figure 6. 7 The relationship between grazing intensity and area of bare rock.

6.4 Summary

- Flower species richness increased with goat grazing, but flower cover was not obviously affected.
- Goat grazing decreased vegetation height and increased the total area of vegetation under 10cm high, but had no clear relationship with the number or size of patches, although patch size tended to increase at higher grazing levels.
- Floral diversity was not significantly affected by the area or size of patches but flower species richness tended to increase with patch size.

- Flower abundance decreased with patch number, and flower species richness tended to be in the same direction.
- About 40% of the recorded patches consisted of rock or bare soil, rather than low vegetation, and the area of bare rock increased with increasing grazing intensity.

6.5 Discussion

In the previous study in Israel (Chapter 4), cattle grazing at moderate levels was found to increase the species richness of flowers, but high grazing levels decreased it again. Likewise, this study shows that at moderate levels of goat grazing the species richness of flowers increases but there is no indication that it decreases again at higher grazing levels. However in this study, only one site had over 50% dung presence. It may therefore be that, in the area studied, grazing was never intensive enough to reduce flower species richness. As in Israel, Greece has a very long history of domestic grazing, so many of the species present must be tolerant of high grazing levels. There may even be local strains of some species which are grazing-adapted. In the areas used in this study, the majority of herbs had prostrate growth forms and were often much smaller than was typical for the species according to the flower guides (Davis *et al.*1965; Blamey & Grey-Wilson 1993), which may be an adaptation to grazing (e.g. Noy-Meir *et al.* 1989; Bowers 1993) or a result of growing in spite of high defoliation rates. If some more intensively grazed sites were surveyed it is probable that the relationship between goat grazing levels and flower species richness would be curved, as was the relationship between cow grazing and flower species richness. This seems

especially likely, since goat grazing has previously been found to be very detrimental to Mediterranean flora (Giorgia *et al.* 1998; Pulina *et al.* 1995).

Flower cover did not increase significantly with goat grazing levels as it did with cow grazing in Israel, although there was a slight positive trend. This relationship may have been clearer if there were more sites with high grazing levels. However it is also possible that goat grazing has quite different effects from cow grazing, and that flower abundance is not affected. For example, more buds may be produced in intensively goat-grazed areas but get eaten before they mature, as was found by Noy-Meir and Briske in 1996, (described in Chapter 1). Goat grazing may also be more difficult to adapt to than cow grazing, since goats bite close to the ground (Harrington *et al.*, 1982) whereas cows cannot eat anything less than 5 cm high (Noy-Meir *et al.* 1989). This means that some prostrate species may survive cattle grazing and be able to increase their flower production due to decreased competition, but the same species would not survive goat grazing.

I did not measure the absolute number of flowers, but only the area they covered. The majority of herb species seen in these highly grazed areas had extremely small flowers. This could mean that overall flower cover was not increased with grazing, even if flower number was.

Overall it seems that goats, like cattle, do increase the proportion of vegetation under 10 cm high, although goat grazing only explained 20% of the variation in patch area. This may mean that other factors, such as soil depth and the proportion of rocks, are more important than grazing in determining patchiness, especially since 37.9% of

patches were actually rock or bare soil. However grazing in itself also increased the amount of bare rock. The fact that much of the area of open patch was made up of rock or bare soil may help explain why the proportion of patch did not significantly affect the flower community. A large amount of the open area may have been grazed to such an extent that soil or rock were exposed even though the site as a whole was not this heavily grazed. It is possible that those areas with shallow soil were more sensitive to grazing and trampling since the underlying rock could easily be exposed, so that although species richness of flowers was increased by grazing overall, the species richness in some of the open patches was decreased.

Since goat grazing increased patch area but did not seem to affect patch number, the main mechanism by which goats create patches may be by eating the woody shrubs around the edges of patches. This would make sense since goats are known to devote most of their time to browzing on woody plant types (Perevolotsky *et al.* 1988; Harrington 1982; Sidahamed *et al.* 1981).

7 Exclosure studies in Israel and Lesvos

7.1 Introduction

Plant species composition is only likely to be altered by relatively long-term changes in grazing intensity, but one of the main threats to bees through grazing is thought to be the immediate removal of inflorescences around peak flowering time (Petanidou and Ellis 1996) which reduces the immediate availability of rewards to bees. If some plant species are selected by grazers over others, or are less tolerant to grazing, they may not flower at all, so that the diversity of rewards would also be reduced. This means that even if an area is only grazed for a short period and the overall diversity and abundance of **plants** is not changed, there may still be changes in flower production which have detrimental effects on the bee community.

The ideal way to look at this would be to introduce grazers to a formerly ungrazed area. Since this was not practical, I set up exclosures in order to look at the short-term effect of **removing** grazing pressure from an area that was heavily grazed beforehand. A pilot study was made in Israel in spring 2000 for which the results are given here. Further exclosures were set up (In both 2 and 17 year post-burn sites) in May 2000, which were to be surveyed the following year and where I hoped to look at changes in shrub cover as well as overall flower abundance and diversity. Since it was not possible to return to Israel I only have data from exclosures set up at the start of spring. Exclosures were also built on Lesvos in 2001 for which the results are given in Section 7.3. In Israel, there were apparent differences in the reaction of vegetation to grazing in sites of different post-burn ages (See Chapters 4 & 5). Hence the exclosures on Lesvos were built both in mature forest and in a recently burnt area to

find out whether the removal of grazers also had different effects in sites of different ages.

Due to time constraints and to problems in obtaining permission to build exclosures only a single exclosure was built in any one habitat. There were also problems with the exclosure built in Israel since cattle broke into it half way through the season. The results presented here therefore are all for single exclosures and should simply be viewed as pilot studies. None of the experiments were repeated and none of the results are in any way conclusive. They simply give some ideas of where further work could be done.

7.2 Exclosure in Israel, 2000.

An exclosure was put up on the 20th of March 2000 in a heavily grazed area of field, adjoining the Mitla site (described in Chapter 2, Section 2.1.1) and surveyed 5 times over the next 50 days (See Chapter 2, Section 2.4.1 for methods). However on day 30 (19th April) cattle broke into the exclosure, and although they were shut out again a day later changes were evident after this time. These results therefore give some indication of the immediate effects of excluding cows from a previously grazed area but are by no means conclusive.

The abundance of flowers in both grazed and protected areas started at a similar level when the exclosure was built, then increased steeply as the spring flowering season began. The increase was much steeper in the protected area (Figure 7.1a) so that the percentage difference between the two areas increased (Figure 7.1 b), though this increase was dependant on just one data point. Between day 25 and day 32, flower

cover decreased in both areas, but this decrease was again much steeper in the protected area so that the difference between the two areas decreased.

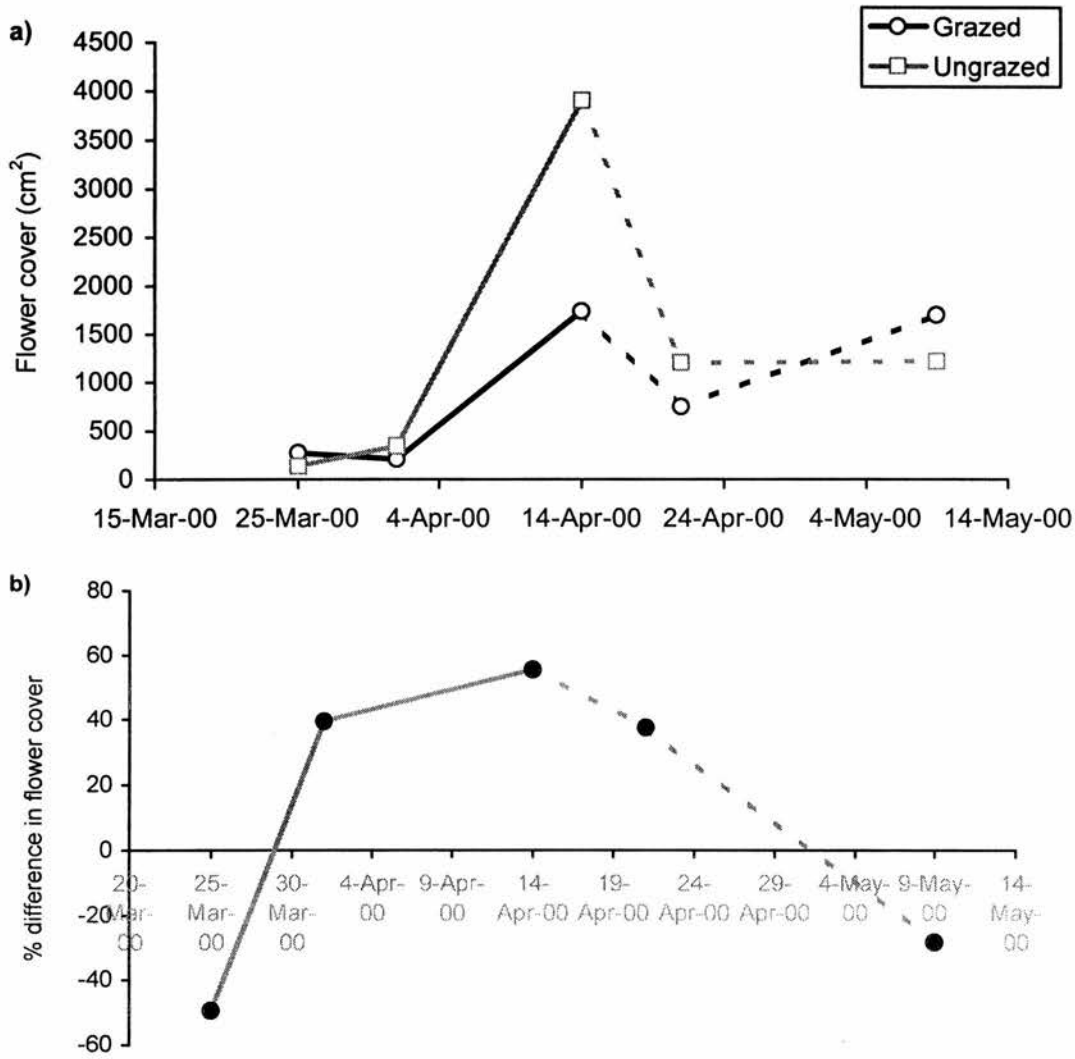


Figure 7.1 a) Change in flower cover over fifty days in grazed and ungrazed areas, b) % difference in flower cover between grazed and ungrazed areas. Dotted lines show time after cattle broke in.

This decline in flower cover in both areas was probably due to a greater number of cows spending time near the exclosure around the 19th of April, when they broke in. Grazing pressure therefore increased, both outside and inside the exclosure, at this time. When the cattle were shut out again, flower cover levelled out inside the exclosure but increased again in the grazed area, so the percentage difference between the two decreased. It seems likely that flower cover would have continued to increase

in the protected area if the cattle had been kept out, but there are not enough data here to be sure of this.

Flower species richness both inside and outside the exclosure increased to start with and then decreased again (Figure 7.2 a). However, in the protected area it continued to increase for about 15 days longer than in the grazed area, so that the difference between the two areas increased steeply. Species richness in the protected area was 32% higher than in the grazed area by the 14th of April (Figure 7.2 b).

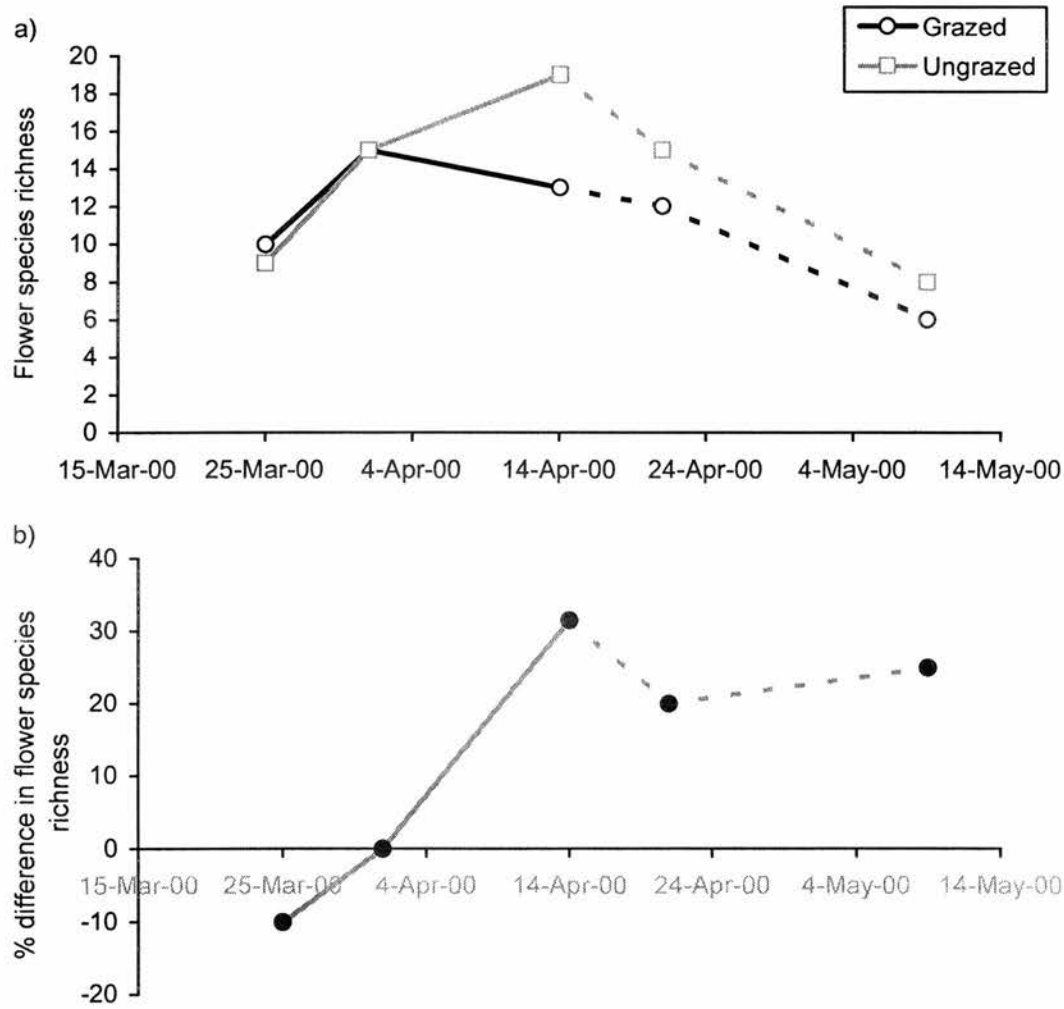


Figure 7.2 a) Change in floral diversity over 50 days in grazed and protected areas, b) % difference in floral diversity between grazed and protected areas. Dotted lines show time after cattle broke in.

Although there was a dip around the time the cattle broke in, the percentage difference between the two areas continued to increase after this until the end of the season.

Again it seems likely that species richness inside the exclosure may have continued to increase for longer, or levelled out, had the cattle not broken in.

Mean vegetation height increased steeply inside the exclosure and although there was a slight decrease when the cattle broke in, it continued to increase throughout the study (Figure 7.3 a). Outside the exclosure, on the other hand, vegetation height remained relatively constant throughout the season, so that the percentage difference between the two areas increased very steeply initially, although it became slightly less steep when the cattle broke in (Figure 7.3 b).

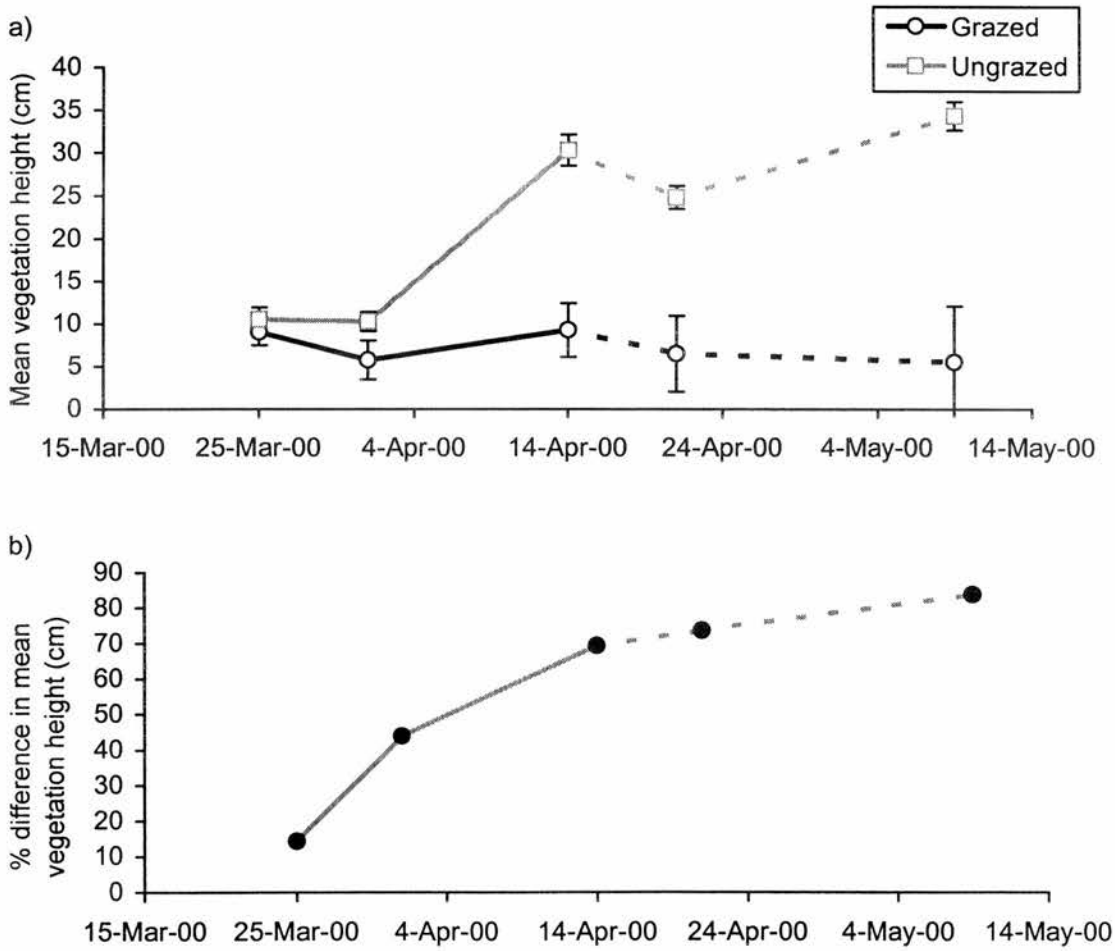


Figure 7.3 (a) Change in mean vegetation height over 50 days in grazed and protected areas. (b) % difference in vegetation height between grazed and protected areas. Dotted lines show time after cattle broke in.

Soil hardness was measured at the end of the season as described in Chapter 2 (2.4.1), to find out whether trampling by cattle increased it. At the end of the season, there was no significant difference in the proportions of hard, medium and soft soil, between the grazed and protected areas (ANOVA: F=0.13, n=40, P=0.723).

7.2.1 Summary of Section 7.2

- Flower cover, flower species richness and vegetation height all increased with protection from grazing until cattle broke into the exclosure.
- Flower cover and flower species richness and vegetation height decreased faster inside than outside the exclosure immediately after cattle broke in.
- Soil hardness was not affected by grazing.

7.3 Exclosures on Lesvos 2001

On the 24th of March 2001, 2 exclosures, each 12m x 10m were set up on the Island of Lesvos, with similar plots marked outside them. One was in a mature *Pinus brutia* forest and the other was in an area burnt 2 years previously. Both areas were grazed by sheep and goats (see Chapter 2, section 2.4.2). In the freshly burnt site, 47% of 200 quadrats contained dung, whereas in the mature site, the value was 21.5 %.

In the recently burnt site, flower cover (Figure 7.4) and flower species richness (Figure 7.5) increased for the first half of the season and then decreased again, both inside and outside the exclosure.

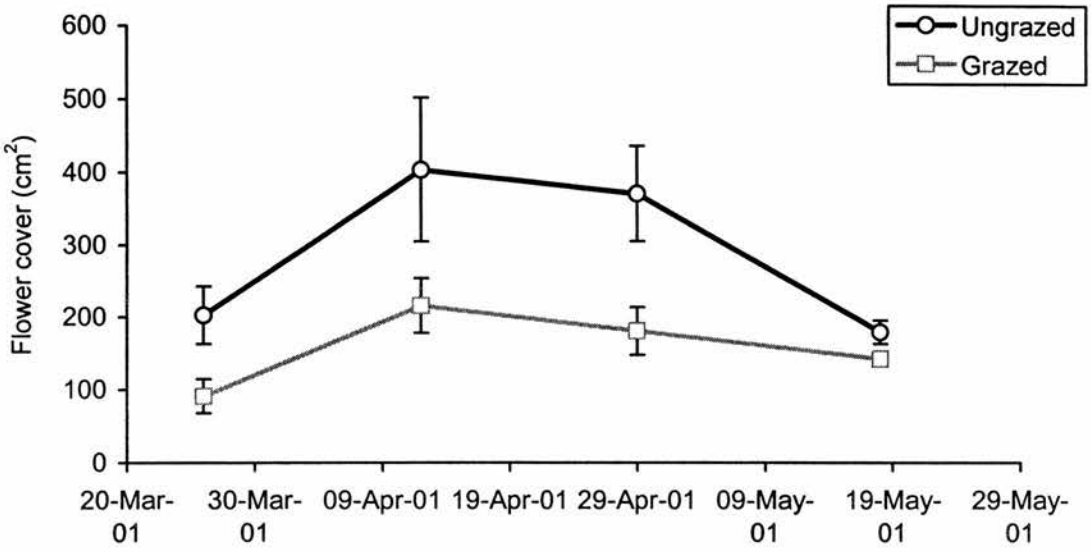


Figure 7.4 Changes in flower cover in grazed and protected plots in the two year post-burn site. Error bars show standard error across the 4 strips surveyed within each exclosure.

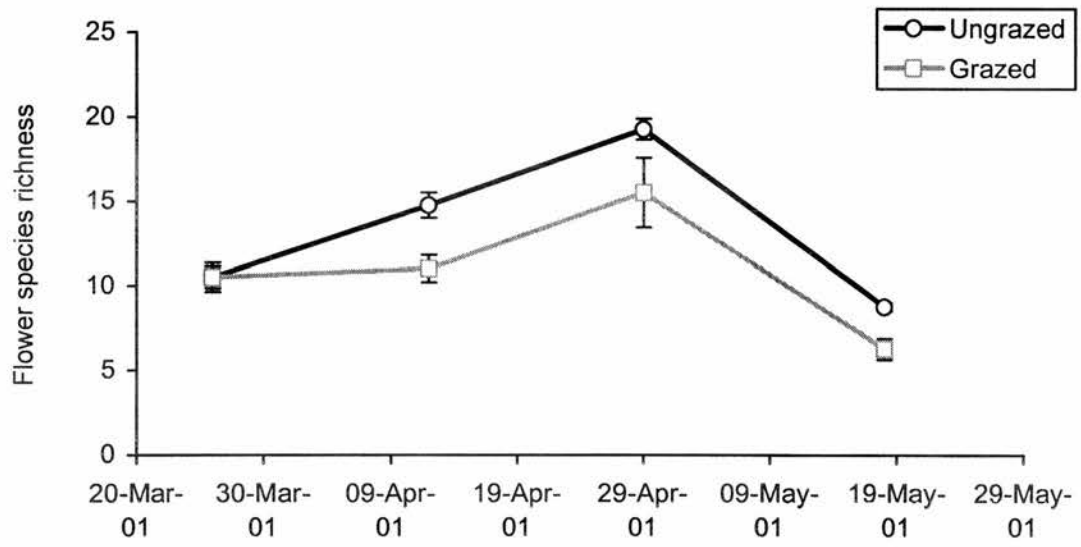


Figure 7.5 Changes in flower species richness in grazed and protected plots in the two year post-burn site

In the mature site, flower cover decreased throughout the season in the grazed area whereas inside the exclosure it stayed level to start with then increased and decreased again (Figure 7.6). Flower species richness decreased throughout the season in a similar manner both inside and outside the exclosure (Figure 7.7), though values were usually higher in the ungrazed exclosure.

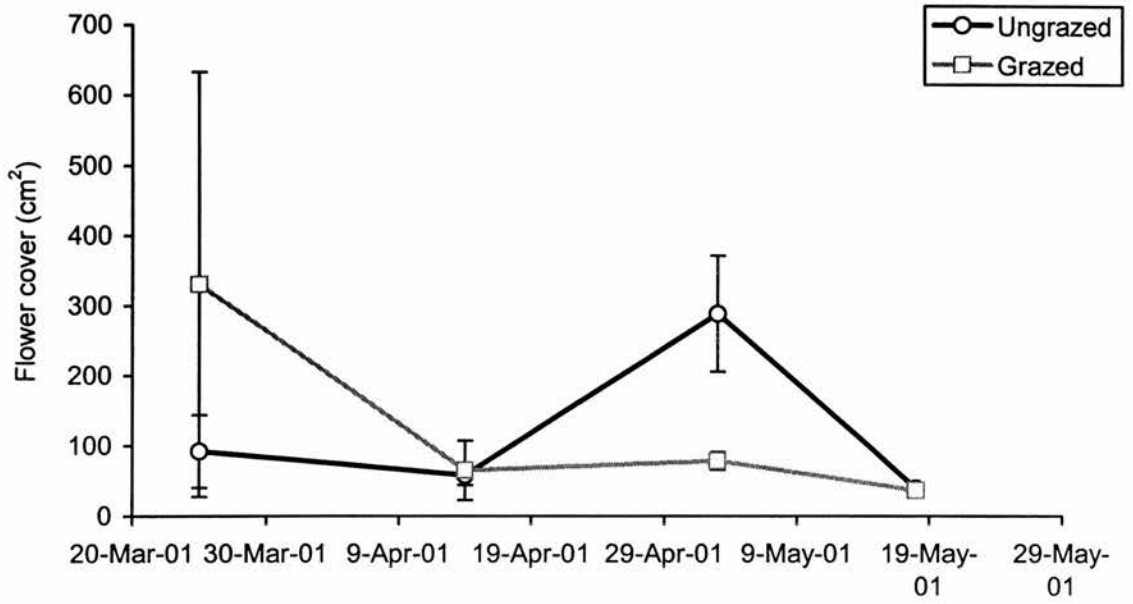


Figure 7.6 Changes in flower cover in grazed and protected areas of mature forest.

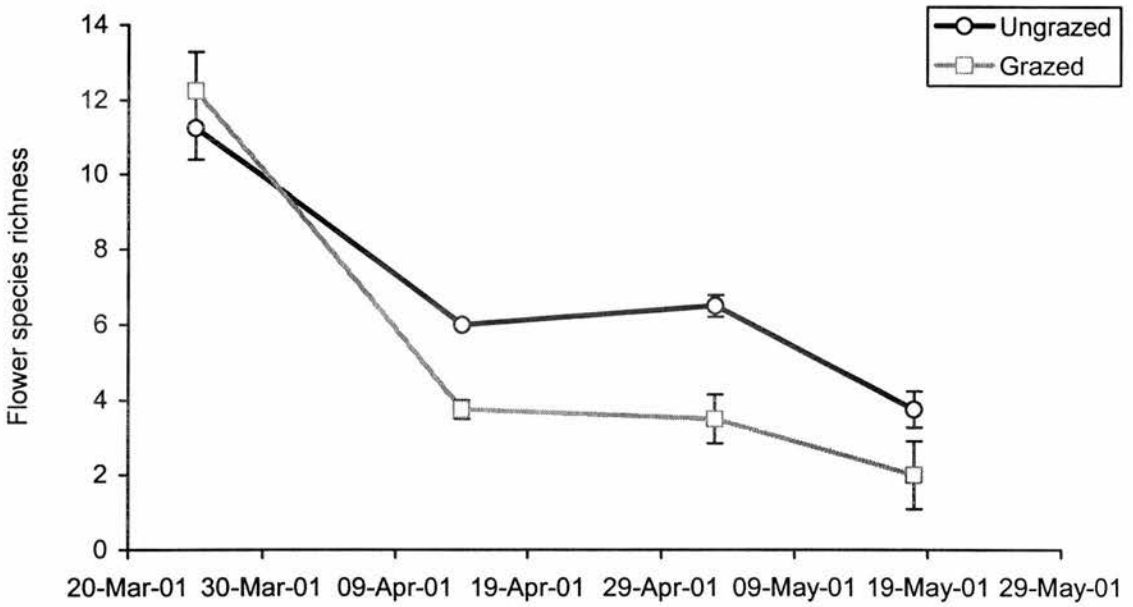


Figure 7.7 Changes in flower species richness in grazed and protected areas of mature forest.

Figure 7.8 shows that the difference in flower cover between grazed and protected areas decreased slightly through the season at the recently burnt site, whereas at the mature site it increased (the last survey should be ignored since there were almost no flowers at all by this time and hence there could be no difference between the two areas).

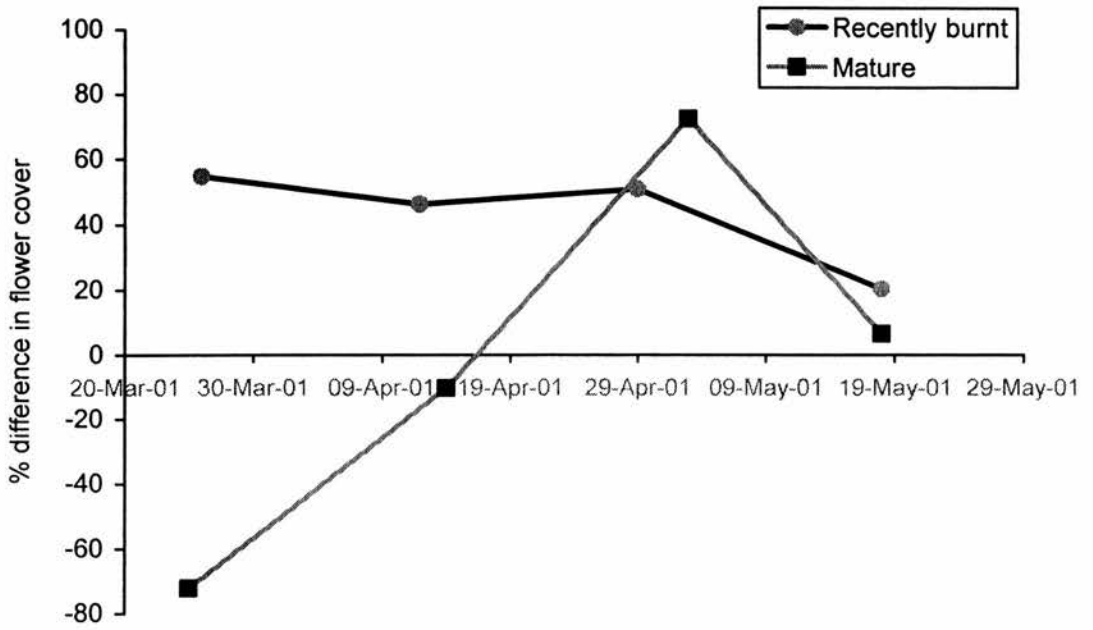


Figure 7.8 The differences in flower cover between grazed and protected areas at a recently burnt site and a mature forest.

The percentage difference in flower species richness inside and outside the exclosures increased immediately at both sites but then levelled out (Figure 7.9).

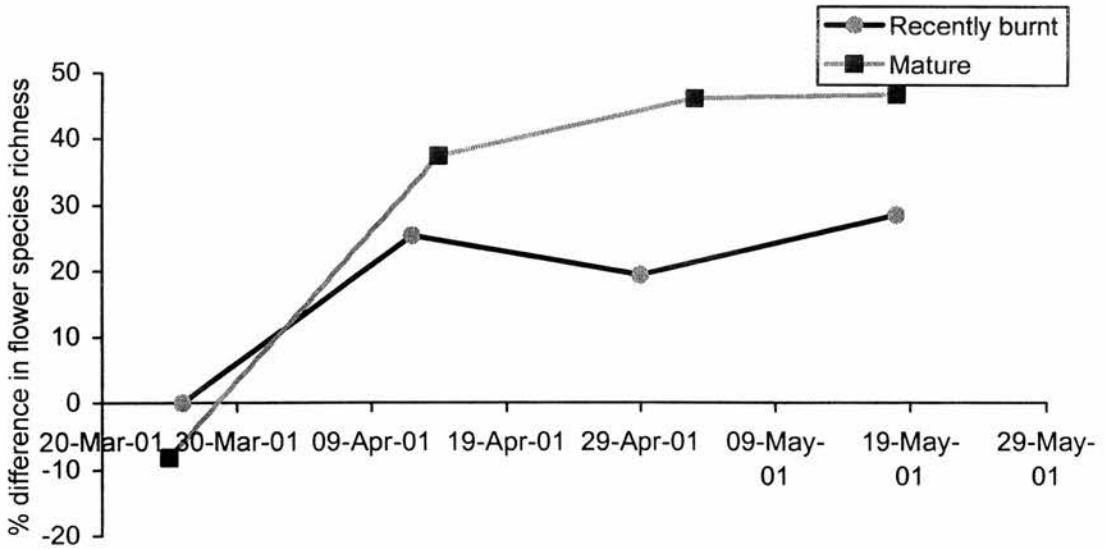


Figure 7.9 % difference in flower species richness between grazed and protected areas at recently burnt and mature sites.

Vegetation height was always greatest in the ungrazed site in both areas, even immediately after the exclosure was built in the recently burnt site. It stayed

relatively level to start with, then increased slightly in both plots in the burnt site (Figure 7.10a), whereas in the mature site (Figure 7.10b) it decreased initially, but then levelled out both inside and outside the exclosure.

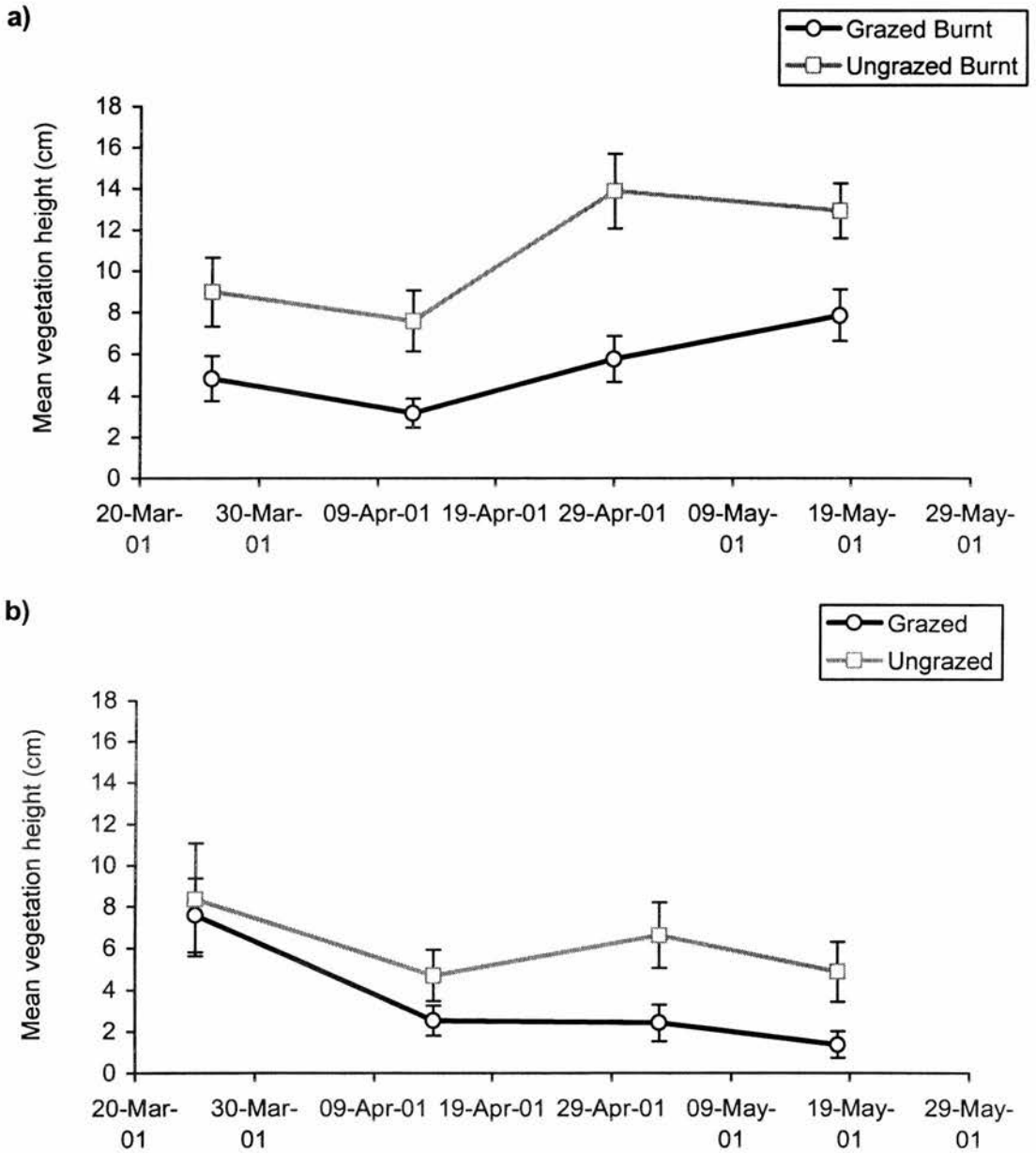


Figure 7.10 Changes in vegetation height in grazed and protected plots a) in the recently burnt site, and b) in the mature forest.

The difference between the grazed and protected areas also stayed relatively level in the burnt site but increased steadily in the mature site (Figure 7.11, R^2=95.7%, n=4, P=0.022).

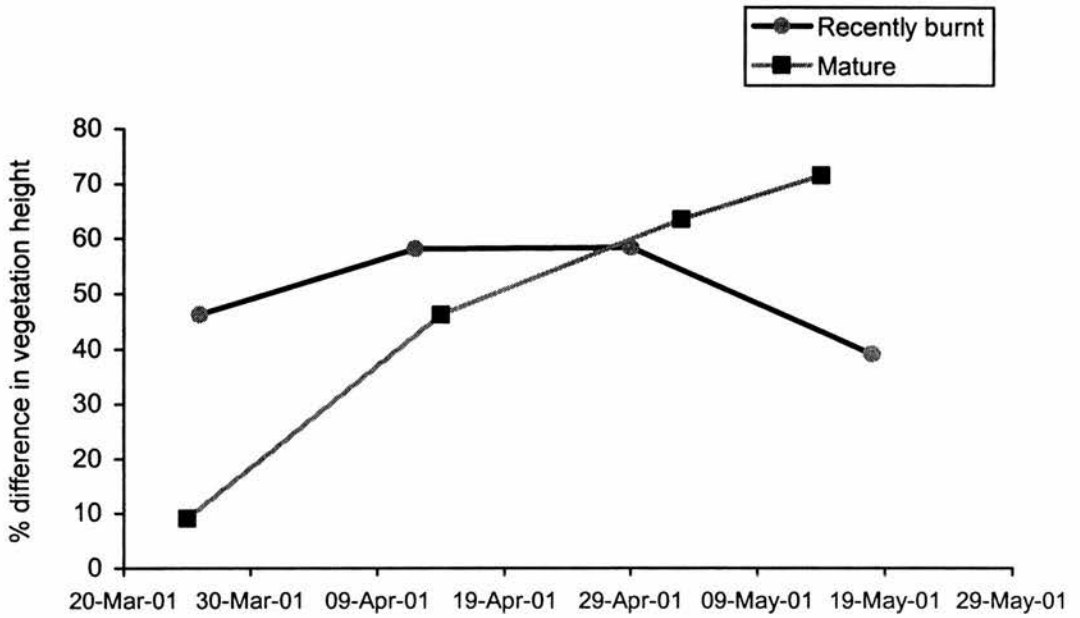


Figure 7.11 Difference between vegetation height in grazed and protected areas in a recently burnt site and in a mature forest.

Soil hardness in both sites was very variable across the season, probably due mainly to the levels of rainfall. The difference between the grazed and protected areas was constant in the burnt site, always being slightly harder outside the exclosure (Figure 7.12). In the mature site, the soil was harder inside the exclosure to start with. The difference between the two plots increased slightly, then decreased so the inside and outside of the exclosure became more similar to each other, i.e. the soil outside the exclosure became slightly harder relative to inside which is what would be expected if soil harness was affected by trampling.

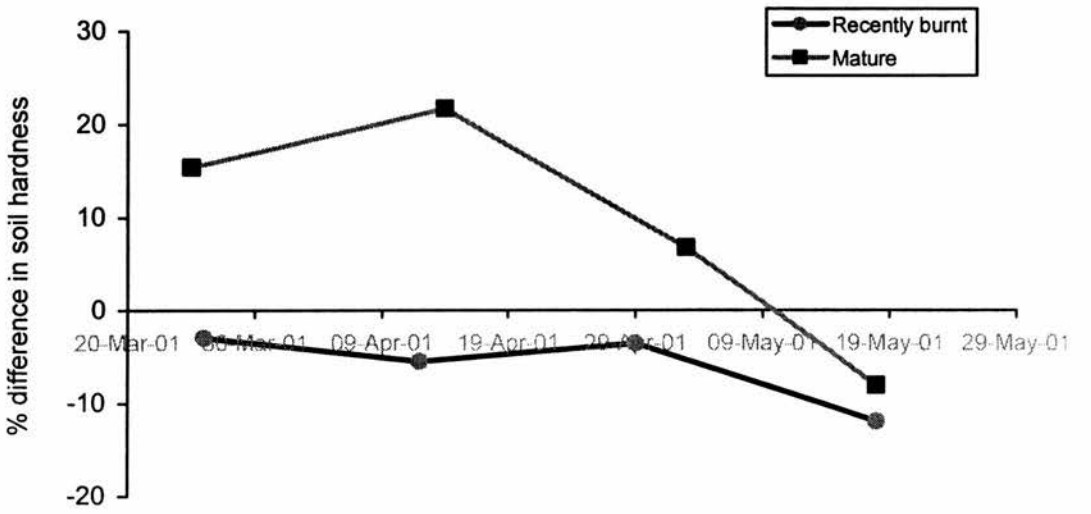


Figure 7.12 Difference between soil hardness in grazed and protected areas in a recently burnt site and in a mature forest.

7.3.1 Summary of Section 7.3

- Protection from grazing seemed to increase flower cover in the mature site, whereas in the burnt site, flower cover decreased slightly when grazers were excluded.
- Flower species richness increased with protection in both areas initially but then levelled out.
- Vegetation height increased with protection in the mature site but stayed level in the burnt site.
- Soil hardness decreased with protection in the mature site, but stayed relatively level in the burnt site.

7.4 Discussion

7.4.1 Exclosure in Israel

The exclosure in Israel suggested that protection from grazing increased vegetation height relative to that in the grazed areas. This is of course unsurprising and fits in with the results described in Chapter 5, where vegetation height was found to decrease with increasing grazing intensity. Although Chapter 4 shows that floral abundance and diversity increase with moderate grazing intensity in the long term, the immediate effects of excluding grazers from a previously grazed area seem quite different. Both the abundance and species richness of flowers increased when grazing pressure was removed. This may be partly because the grazing levels at this site were higher than most of those observed in the main study (Chapter 4); the area around the exclosure had 0.16 dungs m^{-2}, which was comparable with the higher grazing levels studied elsewhere (Shed 2 which was extremely highly grazed had 0.36 dungs m^{-2} but the most heavily grazed plot other than this had 0.14 dungs m^{-2}). Furthermore, the increases in abundance and diversity observed in Chapter 4 are the long-term effects of grazing over several years. There has been time for the actual composition of plants to change as a result of continuous grazing pressure. In working on these exclosures, only diversity and abundance of flowers were looked at, not the diversity and abundance of plants. Many plant species may have been present in both areas but since they were being eaten outside the exclosure they may not have had enough resources to produce any, or as many, flowers as when they were protected. Those flowers they did produce may also have been eaten since some grazers preferentially choose to eat flowers (Anderson *et al.* 1994). Conversely, the plants inside the exclosure were suddenly free of herbivores and had more resources than they

normally would do, allowing them to produce more flowers. If grazing was removed for a longer period, these species may have been out-competed by more dominant species, less able to withstand grazing; but the immediate effect was that they did better than usual.

The situation studied here is unusual since grazing pressure was removed from an area that had already been grazed for 10 years and where many of the plants must have been grazing-adapted species. Adding grazers to a previously ungrazed area might have an even greater impact, since those plants that could cope with grazing would presumably be absent or less abundant.

It was also noticed that the structure of some species was altered in response to grazing. For example, *Cichorium pumilium* grew flattened against the ground outside the exclosure but upright inside. I had intended to follow this up during a third field season in Israel but this proved impossible; thus no data were collected on individual species. However it appeared from casual inspection that, in spite of the different structures, both *Cichorium* plant types had similar flower numbers.

7.4.2 Exclosures on Lesvos

In the mature site on Lesvos, vegetation height increased with protection from grazing, as in Israel. In the recently burnt site, the difference in vegetation height inside and outside the exclosure did not change, even though this site had higher grazing levels than the mature site. The maximum vegetation height reached here, was 14 cm and many of the plants had prostrate forms and were probably grazing-adapted species. These may therefore have already reached their maximum height, so

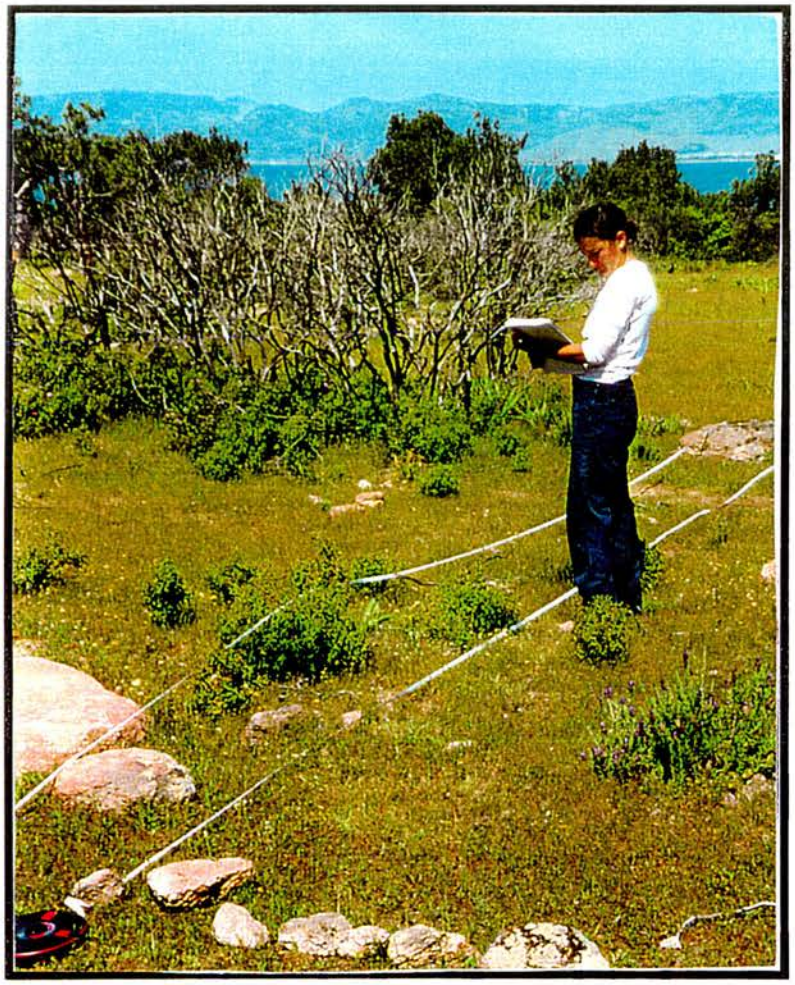
that removing grazing pressure would make little difference. In the long term, these species may be out-competed by other, taller species, but there was no immediate effect.

Flower species richness increased with protection from goat grazing in both areas, and flower cover increased with protection in the mature area. This suggests that flowers or buds outside the exclosure were eaten so plants inside had more resources to devote to flower production as in Israel. However, flower cover in the burnt site did not seem to be affected by the removal of grazing pressure. This could again be because many of the species were grazing-adapted, and able to produce flowers in spite of being grazed. The prostrate forms of most of the herbs in this site, and the very small flowers (described in Section 6.1), suggested that they were indeed mostly grazing-adapted. Since the site had been burnt 2 years before, many of the species may also have been more able to cope with disturbance in general than those in the mature area. Some species must have produced more flowers when protected, explaining the increased species richness inside the exclosure, but these flowers cannot have been abundant enough to make a difference to overall flower cover.

In both sites, soil hardness did seem to decrease slightly when grazing pressure was removed but more clearly so in the mature site. Soil hardness was also much more variable across the season in the mature site. This site had less ground vegetation cover due a layer of pine needles so soil hardness may have been more influenced by the microclimate than the recently burnt site.

7.4.3 Both surveys

Thus overall it seems that exclusion of grazers had similar effects in both goat-grazed and cattle-grazed areas. The main differences were between the different aged sites on Lesvos. On the whole, goat grazing seemed to have less effect in the 2 year post-burn site (Photograph 7.1) than in the mature site. This was true despite the fact that the 2 year post-burn site was more heavily grazed, suggesting that grazing does have different effects in different aged sites. However, as we only had one exclosure in any habitat and the levels of grazing were not the same, these results are not conclusive.



Photograph 7.1 Grazed plot at the 2 year post-burn site near Aschlederi.

Although all the exclosures were in different habitats and none of the experiments were repeated, the general effect of removing grazing pressure from a previously

grazed site seemed to be to increase the abundance and species richness of flowers. Even plants that are well adapted to grazing are able to produce higher numbers of flowers when the pressure is removed. The higher species richness in protected areas shows that some plant species must survive in grazed sites but only succeed in flowering when grazing stops. This has also been shown for an endangered shrub species (*Echinospartum algibicum*) in Southern Spain (Aparicio & Guisande, 1996).

Thus even in areas with a history of grazing, the activity of grazers does inhibit flower production. If grazers were introduced to areas that were previously undisturbed, their impact may be even greater than it was in the sites used in this thesis, and may well be detrimental to bee communities. In the long-term, the ideal management to maintain a high diversity of flowering plants and of bees would be to allow moderate to high levels of grazing through most of the year, as shown in Chapter 4. However, these exclosure studies support the suggestion made previously by Petanidou & Ellis (1996) that the temporary removal of grazers during the main flowering season would be advantageous to bees. Although there is too little data here to be conclusive, trends suggest that the abundance and diversity of flowers can be increased almost immediately if grazers are removed at the start of the flowering season. Since this commonly coincides with the start of peak bee activity the diversity and abundance of bees might also be favoured if grazing pressure was relaxed at this time of year. However this type of management is likely to be impractical for farmers as the flowering season is also when there is most forage is available. Further work would also be needed to show whether this really was advantageous to bee communities.

8. General Discussion

8.1 The effects of grazing on bee diversity and abundance

Previous studies have suggested that grazing animals may have a detrimental effect on bees in South Africa (Gess & Gess 1983) and in California (Sugden 1984, 1985) yet much of this evidence has been anecdotal. More systematic studies of the way grazing affects bee communities have found both positive and negative effects. On Salisbury plain (Carvell 2002) the four most widespread *Bombus* species increased recently grazed areas, and in British farmland (Fussel *et al.* 1991), more bumblebee visits to flowers occurred in areas that were **not** disturbed by grazing. In Swedish pastures (Soderstrom *et al.* 2001) the species richness of bumblebees was negatively associated with grazing intensity. In the Mediterranean basin, which is a known centre of diversity for bee species (Michener 1979; O'Toole 1991; Petanidou & Ellis 1993) and where high levels of grazing have often been seen as a threat to the environment (Petanidou & Ellis 1996; Hill 1998), only Petanidou & Ellis (1996) and Petanidou (1999) have linked grazing animals with bee communities.

Petanidou and Ellis (1996) studied an area of Greek phrygana, west of Athens, which was burned in 1977 and protected from both fire and grazing after this. Flower visitors were observed between 6 and 10 years after the fire, and when further bee diversity measurements were taken using a malaise trap between 14 and16 years after fire, species richness appeared to have declined. This decline was attributed to an absence of management by grazing resulting in a closing of the vegetation and a loss of nesting opportunities. However the results from this study on Mount Carmel showed that bee diversity declined anyway between 10 and 20 years after fire (Potts *et*

al. 2003), and also suggested that malaise traps did not catch as many species of bees as could be caught along line transects (See section 2.1.3), therefore it could have been these factors which caused the decline in bee diversity seen by Petanidou and Ellis (1996).

In the present study, the abundance and diversity of bees were monitored simultaneously at sites with varied grazing levels, several of which were burnt at the same time. The main findings were that in Israeli phrygana, grazing had positive effects on bees in all except the most heavily grazed site. The abundance of bees increased with increasing intensity of cattle grazing, even at relatively high levels. Bee species richness also increased steeply from low to moderate levels of grazing and began to level out at the higher grazing intensities. It was expected that bee species richness would decrease again at very high grazing intensities when few flower species could survive (see section 1.5). However, even at the highest levels of grazing measured in this study, there was no decrease in bee species richness. This was probably because only one small area was so intensively grazed that floral species richness decreased, and although few species of flowers remained in this area, many species of bees still flew through it whilst foraging nearby.

8.2 Grazing affects bees through flowers

Since bees feed almost exclusively on nectar and pollen, the availability of flowers and their rewards were expected to be the main factors limiting bee abundance and diversity. It has been suggested that in phryganic ecosystems, where water is in short supply, nectar is costly to produce and therefore pollen (which has an exceptionally

high energetic value in these communities) may be the main floral reward (Herrera 1985; Petanidou & Smets 1995; Petanidou & Vokou 1990). On Mount Carmel there was an average of 94 times more energy per unit area available from nectar than from pollen but in spite of this, the only significant relationship between floral resource abundance and bees was that between bee abundance and pollen grain number. Similar findings were made by Petanidou & Ellis (1996) in Greek phrygana, where although perennials were the highest nectar producers, they were not visited by more bee species than the annuals.

These results suggest that the crucial issue here is not reward abundance per se. Rather, pollen seemed to be a more *dependable* resource than nectar. All flowers had pollen rewards and these were spread relatively evenly across the sites, whereas flowers with high nectar rewards had a more clumped distribution. Nectar production is very variable depending on time of season, time of day, soil moisture and weather conditions (reviewed by Zimmerman 1988) and may therefore provide very high rewards at certain times but very little at others. Nonetheless, nectar must play some part since bees need an instant supply of energy and water, nectar often being the only source of water in arid environments (Simpson & Neff 1983; Willmer 1988). It may be that on Mount Carmel it was the diversity of nectar sources that was important, as shown by Potts *et al.* (unpublished manuscript). It is also likely that large numbers of flowers such as composites, from which nectar could not be sampled (see chapter 3) and the spatially and temporally variable nature of nectar sources, meant that the sampling regime used was not adequate to give a full picture.

Although the relationships between bees and pollen and nectar resources were not wholly clear, the diversity of bees was very closely related to the diversity of flowers. Herb flowers were the most important group to bees and their diversity and abundance increased at high levels of grazing. This agreed with previous studies in Germany (Gathmann *et al.* 1994; Steffan-Dewenter and Tscharntke 2001) and Costa Rica (Heiathus 1974), where bee diversity was found to be positively related to floral diversity. Path analysis supported the idea that the effects of grazing on bee species richness occurred mainly through changes in the diversity of herb flowers.

Bee abundance was positively correlated with floral abundance and seemed to be more closely related to the previous year's flowers than to the present year's. This agrees with the point made by Tepedino and Stanton (1981), that "the abundance of bees present at one time is the result of investment in young from the previous year's flowers". The abundance of bees has previously been shown to be positively correlated with the abundance of flowers in Germany (Steffan-Dewenter & Tscharntke 2001) and in Central California (Moldenke 1975). However path analysis showed that the increase in bee abundance in highly grazed areas of Mount Carmel was mainly due to an increase in the abundance of halictids, and was not caused by the increased availability of herb flowers as expected (see section 3.1).

The reason that halictids were favoured at high grazing levels was not entirely clear. Neither the overall availability of bare ground for nesting, nor the hardness of the ground was correlated with the abundance of the Halictidae. However it may have been a combination of these two factors that was important since for their nests, halictids require ground that is both bare and compacted enough to burrow in

(Christopher O'Toole pers. com.). Halictid abundance also appeared to be limited to some extent by the abundance of composites, which were more numerous in grazed areas and on which halictids are known to feed, but according to path analysis, composite abundance did not explain the relationship between grazing and halictid abundance. Overall then it was clear that the increases in bee abundance seen in heavily grazed areas were mainly due to increases in the number of halictids, but further work is needed to explain which habitat factors are limiting to these species.

8.3 The effects of grazing on flowers

On Mount Carmel the species richness of flowers was increased by relatively high levels of cattle grazing, and (as predicted in Chapter 1) began to decrease again at the highest levels of grazing measured in this study. This follows the intermediate disturbance hypothesis (Grime 1973; Connell 1978; Huston 1979) but as only one very intensively grazed site was surveyed only the "increasing" side of the curve can be certain. However the results also agree with previous studies of shrublands and woodlands in Israel (Naveh & Whittacker 1979a), where the highest diversity of plants was found at high, but not the highest, grazing levels.

The fact that the optimum grazing level for plant diversity in both these studies occurred at relatively high rather than moderate levels of grazing can be attributed to the long history of domestic grazing in Israel (Naveh and Whittacker 1979a). This has allowed grazing-adapted species to accumulate (McNaughton 1984; Milchunas *et al.* 1988), so that only extremely intensive grazing now causes any reduction in species richness and a relatively high level of grazing is necessary to maintain

diversity. In fact it has been suggested that the great length and intensity of human disturbance in the Mediterranean basin has led to this region having higher plant species diversity than other areas of Mediterranean-type habitat (Naveh & Whittacker 1979). However Fox & Fox (1986) refute the argument that the high resilience of Mediterranean habitats to disturbance is due to their agricultural history and suggest that it is because these ecosystems frequently experience other types of disturbance such as fire and drought.

Milchunas (1988) presented a model of the effect of grazing on grassland communities and predicted that in semi-arid areas with a long evolutionary history of grazing there would be little effect on community composition but that at high grazing levels there would be a slight decrease in diversity. In contrast, the results in this study of Israel showed increases in diversity with increasing grazing intensity in all but the most heavily grazed sites, and were closer to Milchunas' predictions for sub-humid, rather than semi-arid grasslands. A possible explanation is that the main changes in diversity seen in Israel were in the shrubland (phrygana) areas, rather than in grassland areas. Milchunas & Lauenroth (1993) subsequently looked at data from grazed and protected areas around the world and found that in shrublands, the change in species composition with protection from grazing was greater where there was a longer history of grazing, though they did not show whether overall species richness increased or decreased. They also found that species dissimilarity between grazed and ungrazed grasslands was less than between grazed and ungrazed shrublands and that the model they had designed for grasslands (Milchunas *et al.* 1988) underestimated the effects of grazing on changes in species composition of shrublands. This suggested that shrublands are inherently more sensitive to grazing than grasslands are,

but they tend to have other ecosystem attributes which mean that less grazing impact occurs.

The abundance of herb flowers also increased with cattle grazing in the intermediate aged phrygana, and continued to increase even at very high grazing levels, when species richness had already begun to decrease and only those plant species better adapted to grazing remained. The increased abundance in heavily grazed areas was particularly clear for the Compositae, many of which are known to be nitrophiles (Amots Dafni, pers. comm.). These and other grazing-adapted species were able to produce more flowers under heavy grazing where nitrogen levels were increased due to cattle dung and where competition from those species less well adapted to grazing was reduced. This explains why floral abundance continued to increase at levels of grazing higher than that which was optimum for species richness. However, as noted in Chapter 3, many of these species were short-lived, and during the warmest part of the season floral abundance in the most intensively grazed area was very low whereas in less intensively grazed areas there was more continuous replacement of species across the whole season. If more detailed studies were done during each part of the season, one might find that the more heavily grazed areas could not support longer-lived bee species which need a continuity of resources throughout the season (See Petanidou & Ellis 1996).

8.4 The effects of grazing on vegetation structure

The changes in the bee and flower communities discussed so far were all clearest in intermediate-aged phrygana (10-17 years after burning). The effects of grazing were

not clear in sites of other ages (mature forests or recently burnt grasslands). This may have been because they had only very low levels of grazing, or else because grazing had less impact in these areas. In areas with no disturbance by grazing, the lowest levels of floral diversity and the most uniform vegetation structure occurred about 10 years after burning, when a few shrub species, such as *Cistus creticus* and *Calycotoma villosa,* were dominant. Since intermediate-aged sites without grazing were the least diverse, it was conspicuous that disturbed sites of similar age were much more heterogeneous both in vegetation structure and in species composition. As noted by Huston (1994), differences in environmental heterogeneity are almost always correlated with differences in species diversity.

The main effect of cattle grazing in intermediate-aged sites was to inhibit the growth of some of the dominant shrubs, therefore creating or maintaining more open patches, where light-demanding herbs could grow. These open patches increased in number and area where grazing was heavier, allowing a very diverse flora to develop, probably due to the reduced competition from shrubs and to the greater diversity of environmental conditions that exist at patch edges (Smith & Smith 2001). Similar findings were also made in other areas of Israeli phrygana, where herbaceous vegetation cover was negatively correlated with shrub cover (Perevolotsky *et al.* 2001). Studies of *Cistus creticus* and *Lavandula stoechas* in Lesvos (Chapter 5) showed that the number of flowers, and the quantity of rewards they produced, were also increased at the edges of open patches.

The fact that cattle-grazed areas in Israel had lower shrub cover than ungrazed areas, and also greater species richness and abundance of herbs, contrasts with the view that

grazing is a factor in the conversion of grasslands to shrublands, which has been reported in grassland in many semi-arid areas (e.g. Madanay & West 1993; Archer 1995; Kazamaier *et al.* 2001; Skarpe 1990 and references within). This may happen because herbivory reduces above-ground biomass leading to a reduction of fine fuel and fewer grassland fires, therefore favouring the encroachment of woody plants (e.g. Van Auken 2000), or else because after the removal of grasses more water becomes available for trees and shrubs (e.g. Noy-Meir 1982). However, in Mediterranean habitats, grazing has often been shown to slow down shrub encroachment rather than encouraging it. For example, Diaz *et al.* (2001) studied sites in both Argentina and Israel and found that grazing favoured shorter species with small tender leaves and not necessarily those, which like most Mediterranean shrubs, have sclerophyllous leaves. Debussche *et al.* (1996) found that in old-field plots in Mediterranean France plant species richness decreased with age, but that in disturbed plots it remained higher than in undisturbed ones and stayed comparable to younger successional stages. Similarly, grazing slowed down the growth of woody shrubs following fire in Greek phrygana (Giorgia 1998) and on fire-breaks in Israel (Perevolotsky *et al.* 1995) and created more "open" phrygana where the shrub layer was less continuous than in grazed areas (Petanidou and Ellis 1996; Naveh 1982).

In Mediterranean habitats the diversity and abundance of flowers is usually high in the first few years after a fire due to the high contribution of annuals, but without further disturbance diversity decreases again following this flush (Potts *et al.* 2002; Trabaud 1994). However in this study, where cattle were present, a high contribution of herbs (many of which are annuals) was maintained even 17 years after a fire. It seems then, that grazing can slow the "rate of competitive displacement" (see Huston 1994)

by shrubs therefore allowing a high diversity of herbs to co-exist for longer after fire than they would do in less disturbed areas. So whilst intensive grazing may threaten grasslands in some parts of the world by encouraging shrub encroachment, in Mediterranean areas it can have the opposite effect and lead to increases in the diversity of annuals and other herbs. On Mount Carmel it was mainly the species richness of these flowers, which allowed a very diverse bee community to survive in grazed areas.

According to Huston (1979), even slowed rates of competitive displacement lead to competitive exclusion in the end. On the other hand, it seems likely that in this system, the dominant shrubs and trees are prevented from growing at all in some patches so that grazed areas may mature into forests with more clearings than ungrazed areas, therefore increasing diversity even in the long term. Since no information could be obtained on the long-term history of grazing in the mature sites used in this study this idea could not be tested. However there was considerable variation in the number of clearings and open areas in different forests, suggesting that there may have been differences in disturbance levels in the past.

8.5 Conservation in Mediterranean phrygana

Petanidou (1999) states that, since the target of ecological management is normally to achieve and maintain the highest biodiversity within a community, management of Greek phrygana should aim to diminish the perennials (which were shown to have many competitive advantages over annuals in the course of succession) and to augment the abilities of annuals to exist and thrive. Since this study has shown that

the herbaceous plants (mainly annuals) are more important than the perennials in promoting a high diversity of bees, then the management practices which enhance the diversity of annuals will also enhance bee diversity.

The species richness of annuals and of bees on Mount Carmel were both highest at moderate to high levels of grazing, therefore supporting the suggestions for bee-friendly management of Mediterranean phrygana made by Petanidou and Ellis (1996). These authors suggested that in order to preserve the diverse pollinating fauna which exists during the early post-fire stages, Mediterranean phrygana should be burned regularly and that gradients in grazing pressure should also be used to maintain heterogeneity on a finer scale and to enhance nesting opportunities.

If fire is too frequent then floristic diversity can be lost (Esseen *et al.* 1992; Russel-Smith *et al.* 1998) since some species may not have time to flower and set seed (Ne'eman *et al.* 1997). Also some bee species have habitat requirements which exist only in mature forest so it is necessary to allow some areas to mature completely. The results of this study and others (e.g Debussche *et al.* 1996; Perevolotsky *et al.* 1995; Giorgia 1998) show that by using grazing animals, succession can be slowed down therefore maintaining patches with a high contribution of annuals and a more heterogeneous habitat overall. Nevertheless it **has** been shown that if grazing is too heavy in the first winter and spring after a fire, then this can damage the growth of the most palatable trees and encourage more aggressive shrubs (Naveh 1990). The timing of grazing must therefore be taken into account.

Cattle grazing on Mount Carmel at the present levels is almost entirely beneficial to bee communities and could therefore be the ideal way to manage phrygana. Although cattle grazing could be a problem here if it became more intensive, it seems that in Mediterranean phrygana "overgrazing" by cattle is unlikely to occur. The reason for this is that in the summer, all the herbaceous vegetation dries up, leaving only woody shrubs so that cattle have to be given supplementary food (Eli Sandivski, pers. comm.). Hence although cattle may limit the growth of woody shrubs, they do not prevent it altogether. Indeed Perevolotsky *et al.* (1995) showed that in Israel heavy cattle grazing slowed down the growth of woody vegetation, but it still recovered after two years. Also, the fact that cattle find it difficult to eat anything less than 5cm high (Noy-meir *et al.* 1989) means that they are unlikely to clear the vegetation completely, except by very heavy trampling.

It may also be possible to achieve similar results using goats or sheep rather than cattle, as long as great care is taken to prevent grazing pressure from becoming too high. Goat grazing has been seen as a threat to Mediterranean habitats in the past (Giorgia *et al.* 1998; Hill *et al.*1998, Perevolotsky *et al.* 1998) but the studies in Lesvos (reported in Chapter 6) showed that grazing by goats can also increase floral diversity if kept at a moderate intensity. Since goats preferentially feed on woody plants (Perevolotsky *et al.* 1988; Harrington 1982; Sidhamed *et al.* 1981), they may do a better job of reducing shrub density than cattle do; but this, and their ability to bite right to the ground (Harrington *et al.* 1992) may also mean that there is a greater risk of overgrazing.

In areas such as Israel and Greece, the plant-pollinator communities have had thousands of years to become adapted to domestic grazing (Naveh 1982), so relatively high levels of grazing could probably be continued for most of the year. However the immediate effects of grazing are different from the long-term ones. The exclosure studies (Chapter 7) showed that the removal of grazing pressure from previously grazed areas led to an immediate increase in the diversity and abundance of flowers. Grazing during the flowering season seems to prevent plants from producing their maximum potential number of flowers, probably because at this time grazers may remove the actual inflorescences as well as the green parts of the plants. This means that grazing can immediately reduce the availability of resources for bees. As noted by Petanidou and Ellis (1996), only a few plant species continue to flower during the summer and there is little temporal overlap between species at this time. Since longer-lived bee species need the consecutive blooming of several plants to carry them over time, the remaining few flowering species in the summer are essential to support them. The loss of flower species due to grazing during the summer may therefore be more detrimental to bee communities than it would be at other times of the year.

It seems then, that the ideal management to maintain the diversity and abundance of bees and flowers in phrygana would be to allow a moderate level of grazing (which would preserve the mosaic structure of shrubland and open patches), but to avoid excess grazing in the first season after a fire when seedlings and young shoots of the more palatable tree species are likely to be damaged. Ideally, heavy grazing would also be avoided throughout the flowering season but this would be impractical since it is during the spring that the best forage is available for cattle. However the time when grazing is likely to be most detrimental to bee communities is during the summer

when only a few plants species are still flowering (Petanidou & Ellis 1996) and those left are essential to support bees that live throughout the season. The removal of grazers at this time is still likely to be unpopular with farmers since they would need somewhere else to move their cattle to and would probably have to give them more supplementary food than they already do. However the results from Mount Carmel show that even if a relatively high grazing pressure is kept up all the year round, the diversity of bees and flowers is higher than if there is no grazing.

A recent problem in the Mediterranean seems to have been the "overprotection" of areas such as Nature reserves and National parks. Both fire and grazing as well as other anthropogenic disturbances have often been prevented in protected areas as they have been seen only as a threat to the habitat (Naveh 1982; 1990). Complete protection from fire can lead to impoverished plant communities (Bond 1980) and the expansion of flammable forests (Naveh 1990; Schiller *et al.* 1997) so that when fires do occur they can spread across huge areas. Lower levels of grazing can also result in a build up of fuels and increased risk of fire.

Previous studies have shown that protection from grazing can result in vegetation that is very homogenous in structure and where there is little plant diversity (e.g. Naveh & Whittacker 1979; Smart *et al.* 1985; Bowers 1993; Petanidou & Ellis 1996). This study has confirmed these facts and has shown that a lack of grazing can also lead to reduced diversity in the bee community. An obvious example of "overprotection" is Haibar Nature reserve on Mount Carmel which has been completely isolated from domestic grazing. Since the area was burnt in 1989, regeneration has resulted in a thick scrub comprised mainly of *Cistus spp.* and *Catycotoma villosa.* This area has a

very low diversity of both bees and flowers when compared with sites that are just a few years older but heavily grazed.

Mediterranean landscapes consist of very heterogeneous mosaics of semi-natural and agro-pastoral ecosystems which are maintained at different stages of regeneration and degradation (Naveh 1990). This diversity is due to a long evolutionary history of drought, fire and grazing to which the flora and fauna have become adapted. It is therefore necessary that these types of disturbance continue at a certain level in order to maintain the high diversity of plants and animals. However careful management is needed to insure that land use does not become too intensive and lead to habitat degradation.

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Genus	Species	Den981	Den982	Den983	DenNB4	DenNB5	DenNB6	Haibar1	Haibar2	Haibar3	Mit2	Mit3	Mit7	Etz74 1	Etz74 2	Etz74 3	EtzNB4	EtzNB5	EtzNB6	Hod1	Hod2	Hod3
Andrena	sp. 99/01	2																				1
Andrena	sp. 99/02			1									1									
Andrena	sp. 99/03	1	1	1			1															
Andrena	sp. 99/04							1														
Andrena	sp. 99/05																				1	
Andrena	sp. 99/06																	1				
Andrena	sp. 99/07								1													
Andrena	sp. 99/08							1														
Andrena	sp. 99/09	1											1									
Andrena	sp. 99/11		1	1																	1	
Andrena	sp. 99/12																1				1	
Andrena	sp. 99/13																1					
Andrena	sp. 99/15																					1
Andrena	sp. 99/16	1					3											1				1
Andrena	sp. 99/17												1									
Andrena	sp. 99/18				1																	
Andrena	sp. 99/19																				1	1
Andrena	sp. 99/20												1									
Andrena	sp. 99/21																					1
Andrena	sp. 99/22	1												1					1			
Andrena	sp. 99/23																				1	
Andrena	sp. 99/24			1					1				1								1	
Andrena	grandilabris			1		2		3	4	1			1	1	1							
Andrena	nigripes														1							
Andrena	rufomaculata	2	1	1												1	1	1				
Andrena	unicincta					1												1				
Andrena	vetula														2			3				
Mellitiodes	mellitoides					1		1	1													
Melliturga	pristans													2								2
Panurginus	orientalicus																				1	
Anthophora	biciliata														1		1					
Anthophora	dispar		2			1	2		2			2	5								2	
Anthophora	dufourii				1																	
Anthophora	nigriceps								1													
Anthophora	plumipes		1		1		3															
Apis	mellifera	3		7	3	8	1		24	21	2	11	2	12	32	7	22	10	11	47	67	3
Bombus	terrestris											1			1							
Eucera	sp. 99/01	1					1													1		
Eucera	sp. 99/02																					1
Eucera	sp. 99/04		1	1																		
Eucera	sp. 99/05																			1		
Eucera	sp. 99/06		3	2			1							1								
Eucera	sp. 99/07																		1			
Eucera	sp. 99/08		1																	1		
Eucera	sp. 99/11						1															
Eucera	sp. 99/13																			1		
Eucera	aelopus											1										
Eucera	berenice																		1			
Eucera	caerulescens																					2
Eucera	decipiens									1	1			1					3			1
Eucera	helvola																				1	
Eucera	inflexitarsis												1	1								2
Eucera	interrupta																1					
Eucera	laxiscopa																				1	
Eucera	nitidiventris																	2	1			
Eucera	palaestinae														1		1					
Eucera	sulcata												1									
Eucera	transversa	2	4	3	2	2	2	2	1	2			6			2				2	2	4
Habropoda	tarsata	6	3		9	5	7	2	6	8					16	10	5	9	5	4	10	6

Bee species list for 1999, across 5 survey rounds. Numbers show number of individuals of each species caught or identified. N.B. This does not include bees caught of identified in flight.

Genus	Species	Den981	Den982	Den983	DenNB4	DenNB5	DenNB6	Haibar1	Haibar2	Haibar3	Mit2	Mit3	Mit7	Etz74 1	Etz74 2	Etz74 3	EtzNB4	EtzNB5	EtzNB6	Hod1	Hod2	Hod3
Melecta	sp. 99/01				1		1															
Melecta	sp. 99/02													1								
Nomada	sp. 99/01				1		2															
Nomada	sp. 99/02				1																	
Nomada	sp. 99/05																					1
Nomada	sp. 99/07		1																	1		
Nomada	ottomanensis	1																				
Nomada	rubricollis		1	2																		
Synhalonia	plumigera					1									2			1				
Xylocopa	cyanescens			1							1								1			
Hylaeus	sp. 99/01							1														
Hylaeus	sp. 99/02														1							
Hylaeus	sp. 99/03							1														
Hylaeus	sp. 99/06		1										1									2
Hylaeus	sp. 99/07			1		2																
Dufourea	longicornis						1		1	1												
Halictidae	sp. 99/01			1																		
Halictidae	sp. 99/03																					1
Halictidae	sp. 99/04					1			2									1				
Halictus	resurgens																					1
Lasioglossum	caspicum	7	2	3	2	5	1			1	1				1							
Lasioglossum	leucozonium	1	1																			1
Lasioglossum	malachura			1					2	1										1		1
Lasioglossum	marginatum	15	28	28	29	36	16	10	13	13	23	17	11	1	11	2	9	4	3		1	12
Lasioglossum	psuedosphec	1	2			2			1	1											1	1
Lasioglossum	transitorium	4		3																		
Pseudapis	equestris																			1		1
Anthidium	dalmaticum									1												
Anthidium	septemdentatum								1				1								1	
Ceratina	sp. 99/02															1						
Ceratina	sp. 99/03								1													
Chalicodoma	montenegrense														2							
Chalicodoma	sicula							1	1													
Chelostoma	sp. 99/01	1						1		2												
Chelostoma	sp. 99/03												1									
Chelostoma	sp. 99/04													1								
Chelostoma	sp. 99/05				2																	
Chelostoma	sp. 99/06												2									
Chelostoma	sp. 99/07												1									
Chelostoma	sp. 99/09				3					1												
Hoplitis	sp. 99/01																					1
Hoplitis	sp. 99/03																					1
Hoplitis	rufotibialis																				1	1
Hoplitis	stichi																			1		
Megachilidae	sp. 99/01	1		1																		6
Megachilidae	sp. 99/02																				1	
Megachilidae	sp. 99/03	1																				1
Megachilidae	sp. 99/04				1																	1
Megachilidae	sp. 99/05												1									
Megachilidae	sp. 99/06																				1	
Megachilidae	sp. 99/07		1																	1		
Megachilidae	sp. 99/08																			1		
Megachilidae	sp. 99/09																			2	1	
Megachilidae	sp. 99/10																				1	
Megachilidae	sp. 99/11					1												1				
Megachilidae	sp. 99/13																				1	
Problem	sp. 99/01																				1	

Bee species list for 1999, across 5 survey rounds. Numbers show number of individuals of each species caught or identified. N.B. This does not include bees caught of identified in flight.

Site			Bot			Den98			Etz74			EtzNB			Hai 89		
			1	2	3	1	2	3	1	2	3	4	5	6	1	2	3
Family	Genus	Species															
Apidae	Anthophora	biciliata				1											
	Anthophora	crinipes															
	Anthophora	dufourii		1													
	Anthophora	plumipes															
	Anthophora	rogenhoferi															
	Anthophora Total			1		1											
	Apis	mellifera	11	22	8	11	7	7	32	6	13	3	16	13	15	3	15
	Apis Total		11	22	8	11	7	7	32	6	13	3	16	13	15	3	15
	Eucera	berenice		1													
	Eucera	caerulescens															
	Eucera	decipines															
	Eucera	duplicata															
	Eucera	interrupta										1					
	Eucera	laxiacopa															
	Eucera	obsoleta	1	1	1												
	Eucera	plumigera				4	1					1					
	Eucera	sp 2000/1															
	Eucera	sp 2000/11			1												
	Eucera	sp 2000/12															
	Eucera	sp 2000/13															
	Eucera	sp 2000/14			1												
	Eucera	sp 2000/15															
	Eucera	sp 2000/16															
	Eucera	sp 2000/17				1											
	Eucera	sp 2000/18				1											
	Eucera	sp 2000/19															
	Eucera	sp 2000/20						1									
	Eucera	sp 2000/3		1													
	Eucera	sp 2000/5															
	Eucera	sp 2000/8															
	Eucera	sp 2000/9															
	Eucera	sp 2000/g			2												
	Eucera	sp 2000/j															
	Eucera	sp 2000/k															
	Eucera	sp aff. inflexitarsis															
	Eucera	sp aff. spatulata															
	Eucera	stratonice					1										
	Eucera	transversa		1		2	2	1						1		1	
	Eucera	tridactyla															
	Eucera Total		1	4	5	8	4	2				2		1		1	

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

		Site	Hod 98			HodRep			Mit 83			Mit shed				NewNB		
			1	2	3	1	2	3	2	3	7	1	2	3	6	4	5	6
Family	Genus	Species																
Apidae	Anthophora	biciliata																
	Anthophora	crinipes															1	
	Anthophora	dufourii																
	Anthophora	plumipes									8						1	
	Anthophora	rogenhoferi										1						
	Anthophora Total										8	1					2	
	Apis	mellifera	32	22	101	18	15	29		5	9	20	6	13		3	3	1
	Apis Total		32	22	101	18	15	29		5	9	20	6	13		3	3	1
	Eucera	berenice																
	Eucera	caerulescens		2	1						1	1						
	Eucera	decipines		2	2		1											
	Eucera	duplicata			1													
	Eucera	interrupta																1
	Eucera	laxiacopa		1														
	Eucera	obsoleta																
	Eucera	plumigera																
	Eucera	sp 2000/1	1															
	Eucera	sp 2000/11																
	Eucera	sp 2000/12		2														
	Eucera	sp 2000/13		1			1				1							
	Eucera	sp 2000/14																
	Eucera	sp 2000/15											1					
	Eucera	sp 2000/16											1					
	Eucera	sp 2000/17																
	Eucera	sp 2000/18																
	Eucera	sp 2000/19											1					
	Eucera	sp 2000/20																
	Eucera	sp 2000/3																
	Eucera	sp 2000/5			1													
	Eucera	sp 2000/8										1						
	Eucera	sp 2000/9		1	1		1	1										
	Eucera	sp 2000/g											1					
	Eucera	sp 2000/j																1
	Eucera	sp 2000/k										1						
	Eucera	sp aff. inflexitarsis		1														
	Eucera	sp aff. spatulata		1		1												
	Eucera	stratonice																
	Eucera	transversa		1	2		1					7	4					
	Eucera	tridactyla	3	2	3		1											
	Eucera Total		4	14	11	1	5	1			2	10	8					2

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

Site			Bot			Den98			Etz74			EtzNB			Hai 89		
			1	2	3	1	2	3	1	2	3	4	5	6	1	2	3
Family	Genus	Species															
Andrenidae	Andrena	glanaria					1										
	Andrena	grandilabris						1					1	1		2	2
	Andrena	ocreata							1								
	Andrena	oedicnema arjanica															
	Andrena	polita caspica				1											
	Andrena	pyropygia															
	Andrena	rufomaculata				1											
	Andrena	rutomaculata															
	Andrena	sp 2000/2			1												
	Andrena	sp 2000/3													1		
	Andrena	sp 2000/4		2	3												
	Andrena	sp 2000/5			1												
	Andrena	sp 2000/8															
	Andrena	sp 2000/9															
	Andrena	uncinatua					1										
	Andrena	unicincta															
	Andrena	vetula					1	1									
	Andrena Total			2	5	2	3	2	1				1	1	1	2	2
	Melittoides	melittoides				1											
	Melittoides Total					1											
	Melitturga	praestans syriaca															
	Melitturga Total																
Andrenidae Total				2	5	3	3	2	1				1	1	1	2	2
	Melecta	luctuosa															
	Melecta Total																
	Nomada	rubricollis															
	Nomada	sp 2000/1															
	Nomada	sp 2000/3															
	Nomada	sp 2000/4															
	Nomada	sp 2000/5															
	Nomada Total																
	Synhalonia	plumigera	1														
	Synhalonia Total		1														
Apidae Total			13	27	13	20	11	9	32	6	13	5	16	14	15	4	15
Colletidae	Colletes	sp 2000/1		1													
	Colletes Total			1													
	Hylaeus	armeniacus															
	Hylaeus	lineolatus									1						
	Hylaeus	longimaculis						1									
	Hylaeus Total							1			1						
Colletidae Total				1				1			1						
Halictidae	Halictus	berlandi												1			
	Halictus	subauratus															
	Halictus Total													1			
	Lasioglossum	caspicum														1	
	Lasioglossum	Leucozonium clusinum															
	Lasioglossum	lineare					1	1									
	Lasioglossum	marginatum	7	17	24	10	3	5			1	1	6		19	14	24
	Lasioglossum	pygmaeum patulum															
	Lasioglossum	sp 2000/2															
	Lasioglossum	sp 2000/3															
	Lasioglossum Total		7	17	24	10	4	6			1	1	6		19	15	24
	Nomiapis	diversipes				1											
	Nomiapis Total					1											
	Systropha	planidens				3											
	Systropha Total					3											
Halictidae Total			7	17	24	14	4	6			1	1	6	1	19	15	24

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

Site			Hod 98			HodRep			Mit 83			Mit shed				NewNB		
			1	2	3	1	2	3	2	3	7	1	2	3	6	4	5	6
Family	Genus	Species																
Andrenidae	Andrena	glanaria																
	Andrena	grandilabris						1										
	Andrena	ocreata																
	Andrena	oedicnema arjanica			1													
	Andrena	polita caspica	1															
	Andrena	pyropygia	1															
	Andrena	rufomaculata																
	Andrena	rutomaculata												1				
	Andrena	sp 2000/2		1			1											
	Andrena	sp 2000/3			1													
	Andrena	sp 2000/4			1	1					2	1		1				
	Andrena	sp 2000/5										1						
	Andrena	sp 2000/8									1							
	Andrena	sp 2000/9						1										
	Andrena	uncinatua																
	Andrena	unicincta										1						
	Andrena	vetula																
	Andrena Total		2	1	3	1	1	2			3	3		2				
	Melittoides	melittoides																
	Melittoides Total																	
	Melitturga	praestans syriaca	1															
	Melitturga Total		1															
Andrenidae Total			3	1	3	1	1	2			3	3		2				
	Melecta	luctuosa		1														
	Melecta Total			1														
	Nomada	rubricollis																1
	Nomada	sp 2000/1												2				
	Nomada	sp 2000/3		2								1						
	Nomada	sp 2000/4										1						
	Nomada	sp 2000/5			1													
	Nomada Total			2	1							2		2				1
	Synhalonia	plumigera		1										1				
	Synhalonia Total			1										1				
Apidae Total			36	40	113	19	20	30		5	19	33	14	16		3	5	4
Colletidae	Colletes	sp 2000/1																
	Colletes Total																	
	Hylaeus	armeniacus						1										
	Hylaeus	lineolatus																
	Hylaeus	longimaculis																
	Hylaeus Total							1										
Colletidae Total								1										
Halictidae	Halictus	berlandi					1											
	Halictus	subauratus									1							
	Halictus Total						1				1							
	Lasioglossum	caspicum														1		1
	Lasioglossum	Leucozonium clusinum				1												
	Lasioglossum	lineare				4		1										
	Lasioglossum	marginatum	13	1	3	1		1	19	25	44	23	86	62		3		9
	Lasioglossum	pygmaeum patulum						1										
	Lasioglossum	sp 2000/2					1											
	Lasioglossum	sp 2000/3				1												
	Lasioglossum Total		13	1	3	7	1	3	19	25	44	23	86	62		4		10
	Nomiapis	diversipes			1		1											
	Nomiapis Total				1		1											
	Systropha	planidens					3											1
	Systropha Total						3											1
Halictidae Total			13	1	4	7	6	3	19	25	45	23	86	62		4		11

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

Site			Bot			Den98			Etz74			EtzNB			Hai 89		
			1	2	3	1	2	3	1	2	3	4	5	6	1	2	3
Family	Genus	Species															
Megachilidae	Chelostoma	appendiculatum		1							1						
	Chelostoma	sp 2000/4															
	Chelostoma Total			1							1						
	Coelioxys	sp 2000/1															
	Coelioxys Total																
	Creigtonella	albisecta cypriaca											1				
	Creigtonella Total												1				
	Eoanthidium	insulare															
	Eoanthidium Total																
	Heriades	sp 2000/2					2				2		1				
	Heriades	sp 2000/3															
	Heriades Total						2				2		1				
	Hoplitis	hemisphaerica															
	Hoplitis	rufotibialis															
	Hoplitis	scutellaris															
	Hoplitis Total																
	Hoplosmia	ligurica															
	Hoplosmia	sp 2000/1				1											
	Hoplosmia Total					1											
	Osmia	subcornuta															
	Osmia	submicans															
	Osmia	tetradonta			1												
	Osmia	versicolor	1														
	Osmia Total		1		1												
	Protosmia	sp 2000/2															
	Protosmia Total																
	Rhodanthidium	septemdentatum															
	Rhodanthidium Total																
Megachilidae Total			1	1	1	1	2				3		2				
	Calycodoma	siculum															
	Calycodoma Total																
	Habropoda	tarsata															
	Habropoda Total																
	Xylocopa	sp.															
	Xylocopa Total																

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

Site			Hod 98			HodRep			Mit 83			Mit shed				NewNB		
			1	2	3	1	2	3	2	3	7	1	2	3	6	4	5	6
Family	Genus	Species																
Megachilidae	Chelostoma	appendiculatum	1	1	1					1	2		2	1				
	Chelostoma	sp 2000/4										1						
	Chelostoma Total		1	1	1					1	2	1	2	1				
	Coelioxys	sp 2000/1			1													
	Coelioxys Total				1													
	Creigtonella	albisecta cypriaca																
	Creigtonella Total																	
	Eoanthidium	insulare		1														
	Eoanthidium Total			1														
	Heriades	sp 2000/2					2				1							
	Heriades	sp 2000/3					2											
	Heriades Total						4				1							
	Hoplitis	hemisphaerica			1										1			
	Hoplitis	rufotibialis		1														
	Hoplitis	scutellaris						1										
	Hoplitis Total			1	1			1							1			
	Hoplosmia	ligurica					2											
	Hoplosmia	sp 2000/1																
	Hoplosmia Total						2											
	Osmia	subcornuta									1							
	Osmia	submicans		1														
	Osmia	tetradonta									2							
	Osmia	versicolor			1													
	Osmia Total			1	1						3							
	Protosmia	sp 2000/2					1											
	Protosmia Total						1											
	Rhodanthidium	septemdentatum		2														
	Rhodanthidium Total			2														
Megachilidae Total			1	6	4		7	1		1	6	1	2	1	1			
(blank)	Calycodoma	siculum																
	Calycodoma Total																	
	Habropoda	tarsata														1		2
	Habropoda Total															1		2
	Xylocopa	sp.																
	Xylocopa Total																	

Bee species list for 2000 over 3 survey rounds. Numbers show abundances (number of individuals) in each plot.

Species	Den 98 1	Den 98 2	Den 98 3	Den NB 4	Den NB 5	Den NB 6	Hai 89 1	Hai 89 2	Hai 89 3	Mit 83 2	Mit 83 3	Mit 83 7	Etz 74 1	Etz 74 2	Etz 74 3	Etz NB 4	Etz NB 5	Etz NB 6	Hod 98 1	Hod 98 2	Hod 98 3	Presence
Adonis annua	1																				1	2
Ajuga chia	1		1																		1	3
Allium trifoliatum	1	1	1	1	1	1	1			1		1	1		1	1	1	1	1	1		16
Anagallis arvensis	1	1	1	1				1				1	1		1			1	1	1	1	12
Anchusa officinalis	1	1	1																			3
Anemone coronaria	1	1	1	1	1	1	1				1	1					1		1	1	1	13
Anthemis sp												1							1	1	1	4
Arbutus andrachne											1											1
Artedia squamata																				1	1	2
Asphodelus aestivus		1		1	1							1	1	1	1				1	1		9
Bellevalia nivalis			1																			1
Bellis silvestris															1							1
Bupleurum lancifolium																				1		1
Calycotoma villosa				1	1	1	1	1	1		1	1	1	1	1	1	1	1				14
Campanula sp.1																			1			1
Campanula strigosa																			1	1		2
Chrysanthemum coronarium												1										1
Cichorium pumilum																				1		1
Cistus creticus				1	1		1		1	1	1	1			1							8
Cistus salvifolia				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				15
Compositae, sp. 1																				1		1
Compositae, sp. 2	1	1	1										1					1	1	1	1	8
Compositae, sp. 3													1									1
Compositae, sp. 4																						0
Compositae, sp. 5												1										1
Compositae, sp. 6			1																			1
Compositae, sp. 7																			1	1		2
Convolvulus cantibrica			1																			1
Convolvulus coelesyriacus		1																		1	1	3
Convolvulus pentapetaloides			1																1	1		3
Convolvulus scammonia	1	1																				2
Convolvulus sp. A														1								1
Convolvulus sp. B	1	1					1	1				1	1						1	1	1	9
Coronilla scorpoides	1													1					1	1	1	5
Crepis sp 1	1		1	1								1	1						1	1	1	8
Cretega sp. 1							1	1														2
Crupia sp 1													1									1
Cyclamen persicum	1	1	1	1	1	1				1	1	1			1	1	1	1	1	1	1	16
Erodium sp 1																				1		1
Eryngium creticum	1		1			1					1	1	1						1	1	1	9
Euphorbia Helioscopa		1										1									1	3
Euphorbia hierosolymitana												1		1						1	1	4
Fumana arabica			1	1				1				1									1	5
Fumana thymifolia					1	1	1					1		1								5
Fumaria densiflora		1																	1			2
Genista fasselata					1																	1
Geranium rotundifolia												1								1	1	3
Geranium sp. A																						0
Geranium sp. B	1												1		1					1		4
Geranium sp. C																				1		1
Geropogon hybridus																			1	1		2

Flower species list for 1999 over 5 rounds. Numbers show presence or absence for each plot.

Species	Den 98 1	Den 98 2	Den 98 3	Den NB 4	Den NB 5	Den NB 6	Hai 89 1	Hai 89 2	Hai 89 3	Mit 83 2	Mit 83 3	Mit 83 7	Etz 74 1	Etz 74 2	Etz 74 3	Etz NB 4	Etz NB 5	Etz NB 6	Hod 98 1	Hod 98 2	Hod 98 3	Presence
Gladiolus italicus		1							1	1		1		1								5
Gynandris sisyrinchium	1		1																			2
Hippocrepis unisiliquosa	1		1					1							1				1	1		6
Isatis lusitanica									1				1						1	1		4
Isatis sp 1												1							1	1		3
Labiate, sp. 1																				1	1	2
Lathyrus sp 1																				1		1
Leguminosae, sp.1																			1		1	2
Leguminosae, sp.2	1																					1
Leguminosae, sp.3																			1	1		2
Leguminosae, sp.4		1																				1
Leguminosae, sp.5	1																					1
Leguminosae, sp.6	1																					1
Leguminosae, sp.7	1																					1
Leguminosae, sp.8	1																					1
Leguminosae, sp.9	1																					1
Leguminosae, sp.10													1									1
Leguminosae, sp.11				1																		1
Leguminosae, sp.12														1								1
Licotia luhasia												1										1
Linum nodiflorum		1	1					1				1				1	1	1	1	1		9
Linum pubescens	1	1	1	1									1						1	1	1	8
Linum strictum								1				1	1									3
Lotus judaicum	1	1	1	1								1	1						1	1	1	9
Lotus palustris	1	1																				2
Lotus sp.1		1																				1
Lotus sp.2																				1		1
Lotus sp.3	1		1																			2
Lotus sp.4																					1	1
Lotus sp.5										1												1
Lotus tenuis		1																		1	1	3
Mercurialis annua	1	1	1																1	1	1	6
Nigella cilliaris													1						1			2
Ophrys israelitica	1									1												2
Orchis papilionacea/caspia	1	1		1										1								4
Orchis tridentata										1												1
Ornithogalum narbonense							1						1						1	1		4
Pallenis spinosa																			1	1		2
Prasium majus				1	1		1				1	1										5
Ranunculus asiaticus												1								1		2
Ricotia lunaria																			1	1		2
Rubia sp.																			1	1	1	3
Rubia tenuifolia		1	1			1	1	1	1	1	1								1			9
Ruta chalepensis																			1			1
Salvia fruticosa				1	1	1			1				1	1			1	1				8
Salvia hierosolymitana																					1	1
Salvia viridis												1								1		2
Satureja thymbra												1	1			1		1				4
Scabiosa prolifera													1						1	1	1	4
Sedum sp 1				1																		1
Senecio vulgaris	1		1									1		1	1				1	1	1	8

Flower species list for 1999 over 5 rounds. Numbers show presence or absence for each plot.

Species	Den 98 1	Den 98 2	Den 98 3	Den NB 4	Den NB 5	Den NB 6	Hai 89 1	Hai 89 2	Hai 89 3	Mit 83 2	Mit 83 3	Mit 83 7	Etz 74 1	Etz 74 2	Etz 74 3	Etz NB 4	Etz NB 5	Etz NB 6	Hod 98 1	Hod 98 2	Hod 98 3	Presence
Serapias levantina																						0
Sheradia arvensis		1	1																			2
Shereardia sp. 1			1																			1
Silene sp. 2	1	1																	1			3
Silene sp. 3																				1		1
Silybum marianum																				1	1	2
Sinapis arvensis	1																		1	1		3
Stachys palaestina												1						1				2
Stachys sp. 1																			1			1
Stachys zoharyana												1							1			2
Synelcosciadum anichospermum			1	1	1							1	1					1	1	1	1	9
Thrincia tuberosus	1	1	1	1	1		1	1				1		1	1		1		1	1		13
Trifolium campestre													1									1
Trifolium campestre	1	1	1	1									1						1	1	1	8
Trifolium purpureum													1					1		1	1	4
Trifolium repens																			1	1	1	3
Trifolium resupinatum																			1	1		2
Trifolium sp.1																					1	1
Trifolium sp.2																				1		1
Trifolium sp.3																				1		1
Trifolium sp.4																					1	1
Trifolium sp.5																					1	1
Trifolium sp.6			1																	1	1	3
Trifolium sp.7																				1		1
Trifolium sp.8		1											1								1	3
Trifolium sp.9		1																				1
Trifolium sp.10																					1	1
Trifolium stellatum	1																			1	1	3
Tulipa agerensis				1							1											2
UmbelliferA												1										1
UmbelliferB																					1	1
UmbelliferC																			1	1	1	3
UmbelliferD																			1	1	1	3
UmbelliferE																				1	1	2
UmbelliferF																				1		1
UmbelliferG																	1					1
UmbelliferH												1										1
UmbelliferI																			1		1	2
UmbelliferJ		1																				1
Vicia hybrida												1									1	2
Vicia peregrina		1											1						1	1	1	5
Ziziphora capitata												1	1									2

Flower species list for 1999 over 5 rounds. Numbers show presence or absence for each plot.

Species	Bot1	Bot2	Bot3	Den1	Den2	Den3	E74 1	E74 2	E74 3	ENB4	ENB5	ENB6	Hai1	Hai2	Hai3
Adonis annua					1										
Ajuga chia				298	511	584									
Allium staminium															
Allium trifoliatum		26	55	27	458	168	21	67		88	15	87			
Anagallis arvensis	22	4	11	1	273	624									
Anemone coronaria				16											
Anthemis sp.1	14	28	192	21											
Anthiscus lampocarpus															
Anthyllis tetraphylla	12	2	1												
Arbutus andrachne													2		
Trifolium campestre															
Biscutella didyma															
Bunias erucago	4		1												
Bupleurum lancifolium															
Bupleurum nodiflorum	62	27	169												
Calicotoma villosa	119	3			2	16	11	5	15	1	11		79	168	1376
Callendula arvensis	6														
Campanula sp. 1															
Capsella bursa-pastoris			5												
Carophyllaceae, sp. 1															
Catanche lutea															
Centaurea iberica	11														
Centaurium spicatum								1							
Chaetosciadium trichospermum															
Chrysanthemum coronaria		5	3			3									
Cichorium pumilium	9	46	57												
Cistus creticus				49	121	47		35		6	3		1	17	68
Cistus salvifolius					4	4	264	51	81	63	168	79	471	113	966
Compositae sp. 1															
Compositae sp. 2				15	7	7									
Compositae sp. 3															
Compositae sp. 4			8												
Compositae sp. 5					27	6									
Compositae sp. 6															
Convolvulus coelsyriacus	386	161	131												
Convolvulus doricinium						6									
Convolvulus palestinus															
Convolvulus pentapetaloides				1	3										
Convolvulus sp.1	7	36	18												
Convolvulus sp.2				6	55										
Coronilla scorpioides				5		1									
Coronilla sp. 1	3														
Coronilla sp. 2															
Crepis neuteriana	1	22	11												
Crepis sancta							3								
Crepis sp. 1	45	8	131			54									
Cuscuta sp. 1															
Cyclamen persicum		6		14	25	22								8	
Cynoglossum creticum															
Cytisus sp. 1															
Dianthus strictus			2												
Eriyngium creticim/maritimum	23	12	77												
Erodim cicutarium			2												
Erodium gruinum	2	3													
Erodium muschatum															
Erodium sp. 1															

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Species	Hod1	Hod2	Hod3	HodRep1	HodRep2	HodRep3	Mit2	Mit3	Mit7	New1	New2	New3	Shed1	Shed2	Shed3
Adonis annua				2											
Ajuga chia	5	7	22	94		17									
Allium staminium	4														
Allium trifoliatum	19	17	88	21	19	8		5			1	15	13	23	145
Anagallis arvensis	223	395	191	718	25	451		1	13			1	26		3
Anemone coronaria			5						3						
Anthemis sp.1	44	2	4			17	29	17	59				174	28	17
Anthiscus lampocarpus									7						
Anthyllis tetraphylla															
Arbutus andrachne															
Trifolium campestre				2											
Biscutella didyma				2											
Bunias erucago														677	22
Bupleurum lancifolium						4									
Bupleurum nodiflorum									3				3		16
Calicotoma villosa						5	7	1	1			28	71		
Callendula arvensis									3						
Campanula sp. 1	1														
Capsella bursa-pastoris															
Carophyllaceae, sp. 1	6	33		66	1				42						
Catanche lutea									12						
Centaurea iberica														3	9
Centaurium spicatum															
Chaetosciadium trichospermum								3	4						
Chrysanthemum coronaria							2	2					4	111	
Cichorium pumilium						22							4		
Cistus creticus	1		4	15	25	7		9	15	5	16	8			
Cistus salvifolius				4	486	12		1	5	57	7	418			
Compositae sp. 1													85	1	8
Compositae sp. 2															
Compositae sp. 3	43														
Compositae sp. 4															
Compositae sp. 5															
Compositae sp. 6													9		
Convolvulus coelsyriacus													36		76
Convolvulus doricinium															
Convolvulus palestinus		1		18	3	88									
Convolvulus pentapetaloides	32	1		6		1								3	5
Convolvulus sp.1													9	3	8
Convolvulus sp.2				1											
Coronilla scorpioides	1				1										
Coronilla sp. 1	4		2												
Coronilla sp. 2	1	4													
Crepis neuteriana													11	4	
Crepis sancta															
Crepis sp. 1	1	9	4	12		2	57	86	43				11	1	49
Cuscuta sp. 1	2														
Cyclamen persicum	3		14			2			4		4			2	
Cynoglossum creticum						18									
Cytisus sp. 1												12			
Dianthus strictus															
Eriyngium creticim							2						37		7
Erodim cicutarium															24
Erodium gruinum		2		3											
Erodium muschatum									2						
Erodium sp. 1													91	1	6

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Species	Bot1	Bot2	Bot3	Den1	Den2	Den3	E74 1	E74 2	E74 3	ENB4	ENB5	ENB6	Hai1	Hai2	Hai3
Euphorbia helioscopa															
Euphorbia hierosolimitana				4											
Fumana arabica				6	12	9		6	14						
Fumana thymifolia							3	7	4	13					
Fumaria densiflora				3	4	2									
Genista fasselata						9									
Geranium sp. 1		1													
Geranium sp. 2	19	5	1												
Geranium sp. 3															
Geranium sp. 4															
Geranium dissectum						1									
Geranium robertianum				2	1	2									
Geranium rotundifolium			2	3	64										
Geropogon hybridus						3	2								
Gladiolus italicus							3				6	2	1		9
Hedypnois rhagadiolus		1	21												
Helichrysum sanguinium															
Heptaptera crenata															
Hippocrepis unisiliquosa			3												
Hymenocarpus circinatus	6	26	123												
Isatis sp.1															
Labiate, sp. 1										4		9			
Labiate, sp. 2								6							
Lathyrus sp. 1						4									
Lavatera cretica		4													
Lavatera trimestris															
Leduminosae sp. 1				15	1	1									
Leduminosae sp. 2				2											
Leduminosae sp. 3						1									
Linaria chalapensis															
Linum nodiflorum		1				6		8							
Linum pubescens	14	17	2		4	21	5								
Linum strictum								31	1						
Lonicera etrusca										1					
Lotus coronaria					198	1									
Lotus judaeum	32	17	3	13	1	25									
Lotus sp. 1															
Lotus sp. 2						1									
Malva sylvestris			8												
Medicago collinus						4									
Medicago cornuta															
Medicago orbicularis		1	6												
Medicago sp. 1															
Mercurialis				21	29	12									
Micromeria nervosa															
Nigella cilliaris															
Nonea ventricosa	2	3													
Normal convolvulus															
Notobasis syriaca															
Onobrychis chrystagalli			3												
Ophrys sp. 1								4							
Ornithogallum narbonense	11	2	9				3								
Orobanche mutelli															
Pallenis spinosa												2			
Papaver sp. 1															
Papaver subpiriforme															

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Species	Hod1	Hod2	Hod3	HodRep1	HodRep2	HodRep3	Mit2	Mit3	Mit7	New1	New2	New3	Shed1	Shed2	Shed3
Euphorbia helioscopa	43	23	413											3	
Euphorbia hierosolimitana															
Fumana arabica	21			54											
Fumana thymifolia							53	28	285			12			
Fumaria densiflora	4	5	19	7		92									
Genista fasselata							15	5		15					
Geranium sp. 1															
Geranium sp. 2															
Geranium sp. 3														2	
Geranium sp. 4						4									
Geranium dissectum															
Geranium robertianum		1	2										31	2	
Geranium rotundifolium	39														
Geropogon hybridus															
Gladiolus italicus							12	57	59				1		
Hedypnois rhagadiolus													2		3
Helichrysum sanguinium															
Heptaptera crenata		15	3												
Hippocrepis unisiliquosa															
Hymenocarpus circinatus				34		9							13		48
Isatis sp.1	245	368	1												
Labiate, sp. 1				5											
Labiate, sp. 2															
Lathyrus sp. 1													1	2	1
Lavatera cretica	4	1	19												
Lavatera trimestris					1										
Leduminosae sp. 1															
Leduminosae sp. 2															
Leduminosae sp. 3															
Linaria chalapensis			7												
Linum nodiflorum	1	2	21		2				8						
Linum pubescens		42	57	15	1	3	2						45		2
Linum strictum	3	4		9	88										
Lonicera etrusca															
Lotus coronaria															
Lotus judaeum	44	36	5	2	9			18	5				12		15
Lotus sp. 1				3											
Lotus sp. 2															
Malva sylvestris													42	247	
Medicago collinus															
Medicago comuta	1	1	33												
Medicago orbicularis	4	7	144											3	3
Medicago sp. 1	12	6			5	4									
Mercurialis	5	2	16	57		2									
Micromeria nervosa		1													
Nigella cilliaris		2						2	5				3		
Nonea ventricosa		1													
Normal convolvulus													8		
Notobasis syriaca		4													
Onobrychis chrystagalli	1	18	28	2											37
Ophrys sp. 1												7			
Ornithogallum narbonense	15	17											14		5
Orobanche mutelli													5		
Pallenis spinosa	24	55	2	10	26	6			2						
Papaver sp. 1			2		7										
Papaver subpiriforme			4										4	8	

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Species	Bot1	Bot2	Bot3	Den1	Den2	Den3	E74 1	E74 2	E74 3	ENB4	ENB5	ENB6	Hai1	Hai2	Hai3
Pimpinella cretica															
Pistachio lentiscus		94													
Plantago alba															
Prasium major								1							
Prunus ursina															
Quercus calliprinos															
Ranunculus asiaticus	22										5				
Rhagadiolus stellatus	4	26	18												
Ricotia lunaria	48	23													
Rubia sp. 1		175													
Rubia tenuifolia				52	15			67					1		27
Ruta chalepensis										17					
Salvia fruticosa				23	792	7		8		2					
Salvia viridis	2														
Sarcopterium spinosa				12											
Satureja thymbra				7	39		25	1	28	49	41				
Scabiosa prolifera	4		3				5								
Scandix iberica			6												
Scorpiurus muricatus	3	1	1		6	1									
Senecio vulgaris	26	14	3	2	1	18									
Sherardia arvensis	22	5	22	24		126									
Silybum marianum	9		3												
Sinapis sp. 1	19	9	23	32	11	7									
Solanum nigrum															
Sonchus oleraceus				32											
Stachys herzocalcina	33	8	1												
Stachys zoharyana										1	8				
Synelcosciadum anichospermum	78	25	9				16								
Tetragonolobus palestinus		2	6												
Teucrium divaricatum															
Thistle, sp. 1															
Thrincia tuberosa	2			61	4	27									
Tortillis leptophylla						22									
Trifolium campestre				2		24									
Trifolium cleapeatum	17	6	3	2		1									
Trifolium purpureum	3						2								
Trifolium repens					21	2									
Trifolium resupinatum	18	6	51	1											
Trifolium stellatum						2									
Tulipa agarensis															
Umbelliferae, sp. 1					1										
Umbelliferae, sp. 2															
Umbelliferae, sp. 3															
Umbelliferae, sp. 4	28	46													
Unknown sp. 1															
Unknown sp. 2															
Urospermum picroides	9	19	22	1											
Urtica sp. 1															
Velezia rigida															
Verbascum sp. 1				46											
Veronica cymbellaria						1									
Vicia hybrida															
Vicia palestina															
Vicia peregrina				6			1								
Herb total	1036	829	1226	724	1721	1798	61	184	1	94	34	100	2	8	36
Herb SR	38	39	42	29	24	36	10	7	1	4	4	4	2	1	2
Shrub Total	121	97	0	101	970	92	303	114	142	151	223	79	553	298	2410
Shrub SR	2	2	0	6	6	6	4	8	5	7	4	1	4	3	3

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Species	Hod1	Hod2	Hod3	HodRep1	HodRep2	HodRep3	Mit2	Mit3	Mit7	New1	New2	New3	Shed1	Shed2	Shed3
Pimpinella cretica	3			36											
Pistachio lentiscus									11				1		4
Plantago alba	9	6													
Prasium major			4						8	12		37	8		
Prunus ursina													13		
Quercus calliprinos											13				
Ranunculus asiaticus	3	28	4						18						
Rhagadiolus stellatus															1
Ricotia lunaria														48	
Rubia sp. 1	14	78		6		5			4						
Rubia tenuifolia											15	15	2	1	2
Ruta chalepensis	16	13	8	1											
Salvia fruticosa			8							52	75	39			
Salvia viridis	1								5						
Sarcopterium spinosa															
Satureja thymbra									4			169			
Scabiosa prolifera	3	3	118	23	59								4	15	7
Scandix iberica														7	
Scorpiurus muricatus		8		2	2										
Senecio vulgaris	42	11	6	8					7				14		19
Sherardia arvensis	3			19		114			12				7		
Silybum marianum													16	252	2
Sinapis sp. 1	87	34		46	21	24									27
Solanum nigrum					3										
Sonchus oleraceus															
Stachys herzocalcina	21	9	7						1						
Stachys zoharyana				6					5						
Synelcosciadum anichospermun	7	259		865	4	57		9	11				252	15	35
Tetragonolobus palestinus						8								1	
Teucrium divaricatum								2							
Thistle, sp. 1						6									
Thrincia tuberosa							8								
Tortillis leptophylla															
Trifolium campestre	1	6		3											
Trifolium cleapeatum	3		5	12		19							4	3	12
Trifolium purpureum	34	11	17	6	5	6									
Trifolium repens															
Trifolium resupinatum						7							97	4	5
Trifolium stellatum		3	2												
Tulipa agarensis								45							
Umbelliferae, sp. 1															
Umbelliferae, sp. 2			12												
Umbelliferae, sp. 3	5	14	28												
Umbelliferae, sp. 4	263	7	77										52		2
Unknown sp. 1													55		
Unknown sp. 2				2	22										
Urospermum picroides	26	85	36	37	23	3			92			1	3	9	32
Urtica sp. 1														8	
Velezia rigida									1						
Verbascum sp. 1															
Veronica cymbellaria															
Vicia hybrida			7	5											
Vicia palestina		37													
Vicia peregrina														3	
Herb total	1338	1658	1051	2264	328	999	112	247	425	0	20	39	1200	1487	653
Herb SR	47	46	37	38	22	28	7	12	26	0	3	5	38	30	33
Shrub Total	82	36	437	74	511	24	75	44	334	141	111	723	93	3	4
Shrub SR	5	2	5	4	2	3	3	5	8	5	4	8	4	1	1

Flower species 2000, collected over last 3 survey rounds, March to May. Numbers show abundance (cm) in each site.

Site	3A	3B	3C	4A	4B	4C	5A	5B	5C
Alyssum sp 1									
Anagallis arvensis	4	122	103	9.5	9.5	3	3	1	0
Anemone pavonia									
Anthemis rigida									
Anthemis sp. 1									
Bartsia latifolia	0	1	0	0	0	0	0	0	0
Campian sp. 1									
Centaurium maritimum	0	1	0	12	7	7	11	0	0
Centaurium sp. 1				5	1				
Chickweed									
Cichorium pumilium		6							
Cistus creticus	16	3	14	6.5	6.5	1	1	1	2
Cistus salvifolia	0	1	1	0	0	1	1	3	15
Composite 1									
Composite 2									
Composite 3									
Composite 4									
Composite 5		1	2	6					
Composite 6		1							
Composite 7									
Composite 8									
Composite 9					1				
Composite 10									
Composite 11									
Composite 12	1	0	0	5	3	19	1	2	0
Composite 13				62	2				
Composite 14									
Composite 15									
Composite 16									
Cress sp. 1									
Dodder									
Erodium cicutarium	0	0	0	0.5	0.5	0	2	3	0
Erodium sp. 1									
Fumana 1									
Fumana thymifolia									
Geranium robertianum		2		0.5	0.5	1			
Geranium sp 1				2					
Geranium sp. 2				10					
Hedypnois rhagadioloides	3	4							
Hymenocarpus circinatus				4	4		1	7	
Iris sp 1									
Knobly trefoil					3	6			
Lapulla sp.				1					
Lathyrus sp.		1							
Lavandulla stoechas	39	0	59	1.5	1.5	19	2	32	1
Legouisa									
Leontodon tuberosa	0	4	0	1	0	0	1	1	0
Linaria sp.									
Linum sp. 1	1	12	1	111	17	5	15	3	0
Linum sp. 2, Blue	0	2	0	9	0	0	0	0	0
Lotus angustissimus	0	32	1	239	4	58	0	0	0
Lotus conimbricensis	5			1	1	1			
Lotus sp. 1									
Medicago constricta/rigidula									
Muscari neglectum									
Myosotis sp.				0	0				

Site	3A	3B	3C	4A	4B	4C	5A	5B	5C
Ononis macrosperma									
Orchis sancta				7	12				
Ornithgallum sphaerocarpum	0	0	1.5	3	1.5	0	0	0	0
Ornithogallum sp. 1				8	8				
Ornithopus compressus									
Petroraghid									
Pink trifolium sp. 1		1							
Plantago lanceolata	0	0	1	50	50	15	20	50	0
Plantago sp. 1		1		20					
Ranunculus arvensis									
Ranunculus sp. 1				4					
Sandwort									
Scorpiurus sp.	1	1	2	0	0	0	2	1	0
Scorzonera sp.		1			1				
Sedum album				8					
Sedum sp.									
Serapias vomerea		1		1	1				
Sherardia arvensis	0	26	14	18	0	0	0	0	0
Silene sp. 1									
Silene sp. 2								1	
Silene sp. 3									
Sinapis sp. 1									
Tolpis barbata	0	0	0	60	36	9	2	5	0
Torilis sp.	19	0	0	0	4	30	0	0	0
Trifolium sp 1, Red		1							
Trifolium sp 2									
Trifolium sp 3	1		3	4					
Trifolium sp 4	9	1	4	86	132	36	2	3	0
Trifolium sp 5	17	16	12	29	29	8	0	6	5
Trifolium sp 6								24	
Trifolium sp 7		7							
Trifolium sp 8		1							
Trifolium sp 9		3							
Trifolium sp 10									
Trifolium sp 11									
Trifolium stellatum									
Trigonella sp.				1	1			3	
Tuberaria guttata	1	0	4	3	3	1	4	2	0
Umbellifer 1									
Umbellifer sp. 2									
Unknown 1									
Unknown 2									
Unknown 3		38							
Unknown 4	7								
Unknown 5									
Viccia onobrichioides				2					
Viccia sp. 1						2			
Viccia sp. 2									
Viccia sp. 3									
Viccia sp. 4				3	3				

Site	6A	6B	6C	6.5A	6.5B	6.5C	8A	8B	8C
Alyssum sp 1									
Anagallis arvensis	8	0	1	3	3	4	5	0	5
Anemone pavonia									
Anthemis rigida							1	68	10
Anthemis sp. 1									
Bartsia latifolia	0	0	0	0	14	0	0	0	0
Campian sp. 1							1		
Centaurium maritimum	0	0	0	1	6	6	1	2	0
Centaurium sp. 1									
Chickweed							6		
Cichorium pumilium									
Cistus creticus	25	21	6	15	9	13	7	2	0
Cistus salvifolia	20	11	24	0	0	54	0	0	0
Composite 1							3		
Composite 2									
Composite 3			1						
Composite 4									
Composite 5									
Composite 6									
Composite 7						1			
Composite 8									
Composite 9				3					
Composite 10							1		
Composite 11									
Composite 12	3	2	1	14	26	11	1	15	0
Composite 13									
Composite 14					3				
Composite 15						1			
Composite 16									
Cress sp. 1									
Dodder	16							10	
Erodium cicutarium	0	0	0	0	0	0	8	5	3
Erodium sp. 1									
Fumana 1									
Fumana thymifolia									
Geranium robertianum									
Geranium sp 1									
Geranium sp. 2									
Hedypnois rhagadioloides									
Hymenocarpus circinatus			2						
Iris sp 1									
Knobly trefoil									
Lapulla sp.									
Lathyrus sp.									
Lavandulla stoechas	0	0	47	7	0	8	3	3	0
Legouisa									
Leontodon tuberosa	0	4	1	0	4	8	0	1	2
Linaria sp.									
Linum sp. 1	6	2	2	12	9	59	69	36	46
Linum sp. 2, Blue	0	0	0	0	0	0	0	0	0
Lotus angustissimus	2	0	0	1	1	11	3	9	5
Lotus conimbricensis	1					17			
Lotus sp. 1									
Medicago constricta/rigidula									
Muscari neglectum									
Myosotis sp.									

Site	6A	6B	6C	6.5A	6.5B	6.5C	8A	8B	8C
Ononis macrosperma									
Orchis sancta									
Ornithgallum sphaerocarpum	0	0	0	0	0	1	2	1	0
Ornithogallum sp. 1									
Ornithopus compressus			1			1			2
Petroraghid								3	
Pink trifolium sp. 1									
Plantago lanceolata	0	0	0	300	400	860	7	6	9
Plantago sp. 1									
Ranunculus arvensis						1			
Ranunculus sp. 1									
Sandwort							1		
Scorpiurus sp.	0	0	0	0	1	0	0	0	0
Scorzonera sp.									
Sedum album							22	3	4
Sedum sp.								6	2
Serapias vomerea					1				
Sherardia arvensis	0	0	0	0	1	0	2	17	0
Silene sp. 1								2	
Silene sp. 2									
Silene sp. 3									4
Sinapis sp. 1									
Tolpis barbata	2	1	0	13	6	11	36	51	1
Torilis sp.	0	0	0	3	0	0	0	0	0
Trifolium sp 1, Red									
Trifolium sp 2							13		2
Trifolium sp 3					3	5	5	2	
Trifolium sp 4	76	1	2	3	10	8	2	5	801
Trifolium sp 5	25	12	3	5	6	21	10	1	4
Trifolium sp 6									
Trifolium sp 7									
Trifolium sp 8									
Trifolium sp 9									
Trifolium sp 10									
Trifolium sp 11									
Trifolium stellatum					4	14	3		
Trigonella sp.									
Tuberaria guttata	0	1	0	2	3	6	0	6	0
Umbellifer 1									
Umbellifer sp. 2				4					
Unknown 1								2	
Unknown 2									
Unknown 3									
Unknown 4									
Unknown 5							1		
Viccia onobrichioides									
Viccia sp. 1									
Viccia sp. 2									
Viccia sp. 3									
Viccia sp. 4									

Site	7A	7B	7C	7.5A	7.5B	7.5C	9A	9B	9C
Alyssum sp 1							1		
Anagallis arvensis	1	3	2	45	1	36	6	0	0
Anemone pavonia				5	1				
Anthemis rigida							17		
Anthemis sp. 1						12			
Bartsia latifolia	0	0	0	14	0	1	0	0	0
Campian sp. 1									
Centaurium maritimum	0	11	2	5	0	0	0	0	1
Centaurium sp. 1									
Chickweed									
Cichorium pumilium									
Cistus creticus	25	16	13	9	7	6	3	4	1
Cistus salvifolia	3	3	0	0	0	0	0	0	0
Composite 1									
Composite 2							67		
Composite 3									
Composite 4							1		
Composite 5									
Composite 6									
Composite 7									
Composite 8							5		
Composite 9									
Composite 10								1	
Composite 11				111	12				
Composite 12	6	18	28	2	0	0	17	2	0
Composite 13									
Composite 14									
Composite 15									
Composite 16							23		
Cress sp. 1								14	
Dodder									
Erodium cicutarium	0	1	2	5	2	4	1	2	0
Erodium sp. 1							5		
Fumana 1									2
Fumana thymifolia	1								
Geranium robertianum									
Geranium sp 1								1	
Geranium sp. 2									
Hedypnois rhagadioloides								1	
Hymenocarpus circinatus							20		
Iris sp 1				5					
Knobly trefoil			2						
Lapulla sp.									
Lathyrus sp.									
Lavandulla stoechas	236	0	0	18	7	0	2	6	3
Legouisa							6		
Leontodon tuberosa	2	1	0	7	20	2	1	0	0
Linaria sp.								1	
Linum sp. 1	76	165	48	37	90	22	40	8	20
Linum sp. 2, Blue	4	0	0	1	0	0	1	0	0
Lotus angustissimus	0	0	0	54	16	160	2	0	0
Lotus conimbricensis				7	32				
Lotus sp. 1									
Medicago constricta/rigidula								2	
Muscari neglectum				8					
Myosotis sp.									

Site	7A	7B	7C	7.5A	7.5B	7.5C	9A	9B	9C
Ononis macrosperma	1								
Orchis sancta									
Ornithgallum sphaerocarpum	0	1	1	0	0	3	3	0	0
Ornithogallum sp. 1									
Ornithopus compressus				5	120			3	
Petroraghid									
Pink trifolium sp. 1									
Plantago lanceolata	0	100	1100	200	1000	282	275	10	1
Plantago sp. 1			2						
Ranunculus arvensis									
Ranunculus sp. 1									
Sandwort									
Scorpiurus sp.	6	1	0	0	0	2	0	0	0
Scorzonera sp.									
Sedum album				56	20		15		
Sedum sp.									
Serapias vomerea					2	2			
Sherardia arvensis	0	0	0	0	0	3	0	0	0
Silene sp. 1							2		
Silene sp. 2									
Silene sp. 3									
Sinapis sp. 1				1	5	26			
Tolpis barbata	7	1	13	1	4	8	1	8	5
Torilis sp.	0	1	0	0	0	0	0	1	0
Trifolium sp 1, Red									
Trifolium sp 2									
Trifolium sp 3	4		1	2	124	2			1
Trifolium sp 4	4	4	0	1	0	3	26	17	40
Trifolium sp 5	14	1	1	18	6	6	3	17	0
Trifolium sp 6								16	20
Trifolium sp 7									
Trifolium sp 8									
Trifolium sp 9									
Trifolium sp 10							4		
Trifolium sp 11							30	19	
Trifolium stellatum									
Trigonella sp.									
Tuberaria guttata	1	0	0	1	0	3	2	0	0
Umbellifer 1								1	
Umbellifer sp. 2									
Unknown 1									
Unknown 2				1	4				
Unknown 3									
Unknown 4									
Unknown 5									
Viccia onobrichioides									
Viccia sp. 1									
Viccia sp. 2						3			
Viccia sp. 3						1			
Viccia sp. 4									